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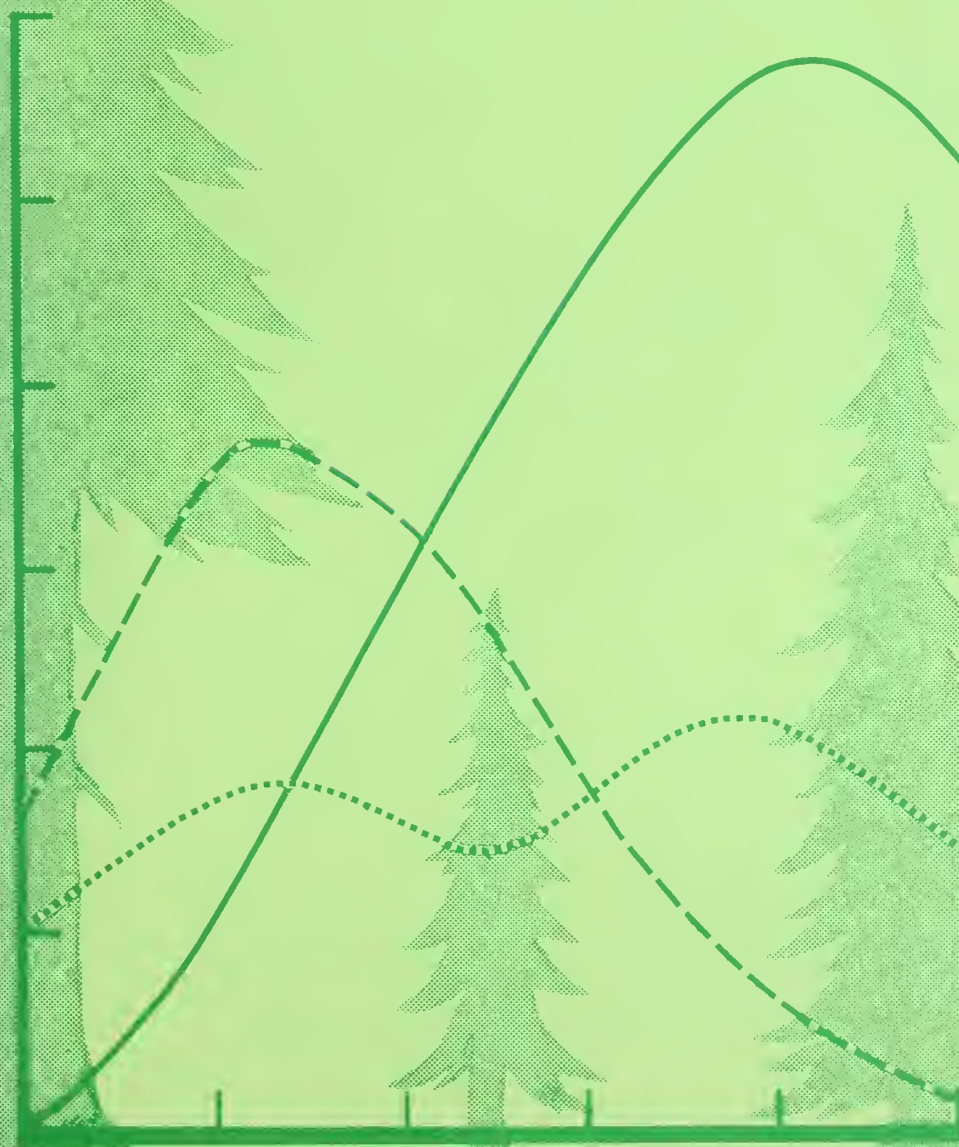
Intermountain
Forest and Range
Experiment Station

General Technical
Report INT-111

April 1981

Modeling Seasonal Abundance of Douglas-Fir Beetle in Relation to Entomophagous Insects and Location in Trees

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ACKNOWLEDGMENTS

We thank Dr. David A. Hamilton Jr., USDA Forest Service, Moscow, Idaho, and Dr. R. Ladd Livingston, Idaho Department of Public Lands, Coeur d' Alene, for reviewing the manuscript. Representative adult insect specimens were identified by the following specialists: *Coeloides* by Dr. C. F. W. Muesebeck, SEL, Beltsville, Md.; *Medetera* by F. C. Harmston, Salt Lake City, Utah; *Enoclerus* and *Thanasimus* by Dr. W. F. Barr, University of Idaho; *Roptrocerus* and *Cecidostiba* by Dr. B. D. Burks, SEL, Beltsville, Md.; and *Belosta* by Dr. L. P. Kelsey, University of Delaware. Dr. R. B. Ryan, USDA Forest Service, Corvallis, Oreg., provided the pictures of *Coeloides*.

RESEARCH SUMMARY

Distributions of Douglas-fir beetles and entomophagous insects were sampled weekly at 3 m intervals on stems of trees. Regression models were developed for predicting abundance of Douglas-fir beetles in relation to entomophagous species, date, and sample characteristics. The logistic function was used to define the probability of the presence of entomophagous insects on samples. An average of 58 percent mortality of Douglas-fir beetle progeny was attributed to entomophagous insects. Suggestions are given on locations of samples and number of samples needed for a given precision of estimate for Douglas-fir beetle and entomophagous species.

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INTRODUCTION

Infestations of the Douglas-fir beetle *Dendroctonus pseudotsugae* Hopk. cause great economic losses of its principal host, *Pseudotsuga menziesii* [Mirb.] Franco (Furniss and Orr 1978). Mature trees are commonly killed after predisposing factors such as windstorms and droughts enable the beetle population to increase.

The Douglas-fir beetle develops through its four life stages (fig. 1) hidden under the bark of its host tree. Most beetles overwinter as callow adults, then fly and infest other Douglas-fir trees during spring. The females bore into the bark and excavate unbranched egg galleries upward in the phloem for an average distance of 15 to 20 cm. The density of egg galleries ranges from 5 to 12 per 0.1 m² in standing trees. Eggs are laid alternatively on opposite sides of the gallery at a rate of 3.1 per cm in Idaho. Eggs hatch in a week or two. The larvae then mine fanlike (fig. 2) from the egg gallery. Larvae complete their mines in a month or so, then construct cells in which they transform to pupae for a brief time before becoming adults. Death of the tree results from a combination of girdling by larvae and the action of microorganisms associated with the beetle.

Distribution of beetles and entomophagous insects in trees was investigated in central Idaho (Kline 1963) as a part of a long-term study of population dynamics by Furniss. That thesis presented graphically the abundance of these organisms by sampling height and date. In this paper, we utilize regression analyses and the logistic function to relate quantitatively the Douglas-fir beetle population density to the number of predators and parasites in relation to time and location in trees. The improved methods provide a means of expressing relationships that previously were either not recognized or incapable of definition. This infor-

mation will facilitate the evaluation of Douglas-fir beetle infestations for such purposes as predicting trend of population and damage, relating Douglas-fir beetle populations to factors affecting tree susceptibility; and will aid in developing improved sampling procedures.

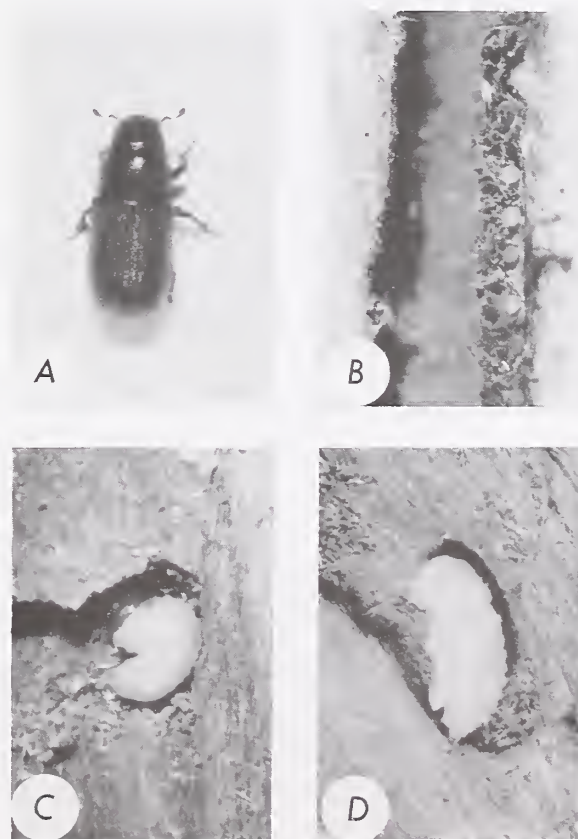


Figure 1.--Douglas-fir beetle life stages.
(A) adult; (B) eggs in gallery; (C)
larva; (D) pupa.

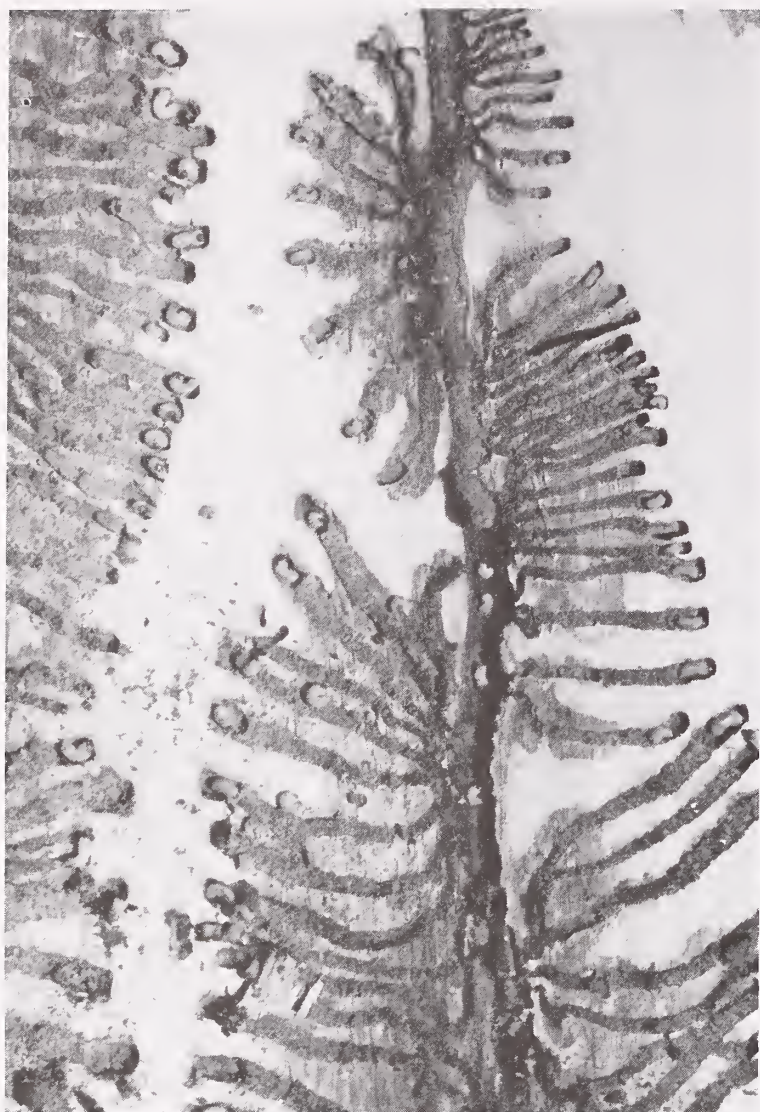


Figure 2.--Douglas-fir beetle egg gallery and larval mines.

METHODS

The study was scheduled to begin when sufficient time had elapsed after beetle attack to reveal trees that were going to die. We thereby eliminated tree resistance as a source of mortality to beetle progeny, and galleries were nearly completed, which resulted in less variation in weekly measurements.

Five infested trees were felled weekly for sampling beginning June 30, 1960. Sampling ended September 2. Samples (fig. 3) were taken at 3 m intervals, beginning 1.5 m above ground to a diameter of 20 cm. Numbers of entomophagous insects were measured on a 15 cm x 30 cm sample, but because Douglas-fir beetle galleries, ventilation holes, and progeny were more abundant, they were measured on an adjacent 93 cm² circular sample cut with a bark punch (Furniss 1962a). Other data obtained at each sample location were: diameter of trunk, bark thickness, and height of sample.



Figure 3.--Comparison of samples. Circular sample was used to measure Douglas-fir beetle galleries and progeny; rectangular sample was used to count entomophagous insects on adjacent area.

Analyses

We used actual sample values rather than converting data to a common area basis. Thus, all counts of entomophagous insects are on a 15 cm x 30 cm (0.45 m²) basis whereas densities of Douglas-fir beetle progeny and length of egg galleries are on a 93 cm² basis.

To estimate rates of survival of Douglas-fir beetles from predation and parasitism, we used ratios of numbers of Douglas-fir beetle progeny to the total length of egg galleries. Initial beetle population (eggs) is related to egg gallery length (Furniss 1957), there being an average of 3.1 eggs/cm.

Simple linear regression was used to relate Douglas-fir beetle population indices to entomophagous insects. To determine the variation explained by regression models, we calculated multiple regression coefficients (R^2).

The following list of variables was considered a basic set for the presence or absence of entomophagous insects: date, height, length of egg galleries, maximum bark thickness, diameter, and number of ventilation holes. Transformations of those variables were also tested in the model building.

In developing the model, the response was fitted to the entire list of variables first. Coefficients in the model were tested for significance by Student's t-test. Variables with nonsignificant ($\alpha < 0.05$) coefficients were deleted and the coefficients for the remaining variables were recomputed.

The logistic function (Walker and Duncan 1967) was used to define the probability of the presence of entomophagous insects using Hamilton's (1974) program. The goodness of fit of the predicted and observed values was tested by chi-square analysis.

Relationships of dependent (e.g., number of Douglas-fir beetles) and independent (e.g., number of entomophagous insects) variables were portrayed with an HP9820 calculator/plotter. The same device was used to plot the logistic function relating entomophagous insects (*Coeloides* or *Medetera*) and sample characteristics.

The efficiency of sampling beetle progeny at 1.5 m and 4.6 m above ground was compared by the degree to which their means were correlated with tree means. Numbers of samples needed to estimate average gallery length, beetle progeny, or entomophagous insects were calculated for a 0.20 coefficient of variation of the mean ($CV_{\bar{x}}$) using the formula $n = (CV_{\bar{x}}/0.20)^2$. This is equivalent to setting sample size for a desired relative variance (Kish 1965).

BIONOMICS OF SPECIFIC PREDATORS AND PARASITES

The insect enemies of the Douglas-fir beetle found in this study are discussed in the general order of their density on samples.

COELOIDES VANCOUVERENSIS [Dalla Torre]

In thin bark portions of trees, *C. vancouverensis* (= *brunneri* Viereck) can be very effective in parasitizing a large percentage of the Douglas-fir brood (fig. 4B) (Ryan and Rudinsky 1962). For instance, Bedard (1933) reported an average of 29 percent of beetle larvae were parasitized, varying from 0-10 percent in the base to 70-95 percent in the top.

Females deposited eggs through the bark (fig. 4A) onto beetle larvae, beginning in early July. By the end of July the parasite was found frequently in trees. Due to a different rate of development, some parasite progeny overwinter as larvae. Others mature and emerge in August to lay eggs on other beetle larvae. The proportion of fast-developing adults may be 95 percent in western Oregon (Ryan and Rudinsky 1962) or a small minority in northeastern Washington (Bedard 1933). Each *C. vancouverensis* larva consumes only a single beetle larva, so the number of *C. vancouverensis* larvae (or their cocoons which are easily counted) equals the number of bark beetle larvae that have been parasitized.

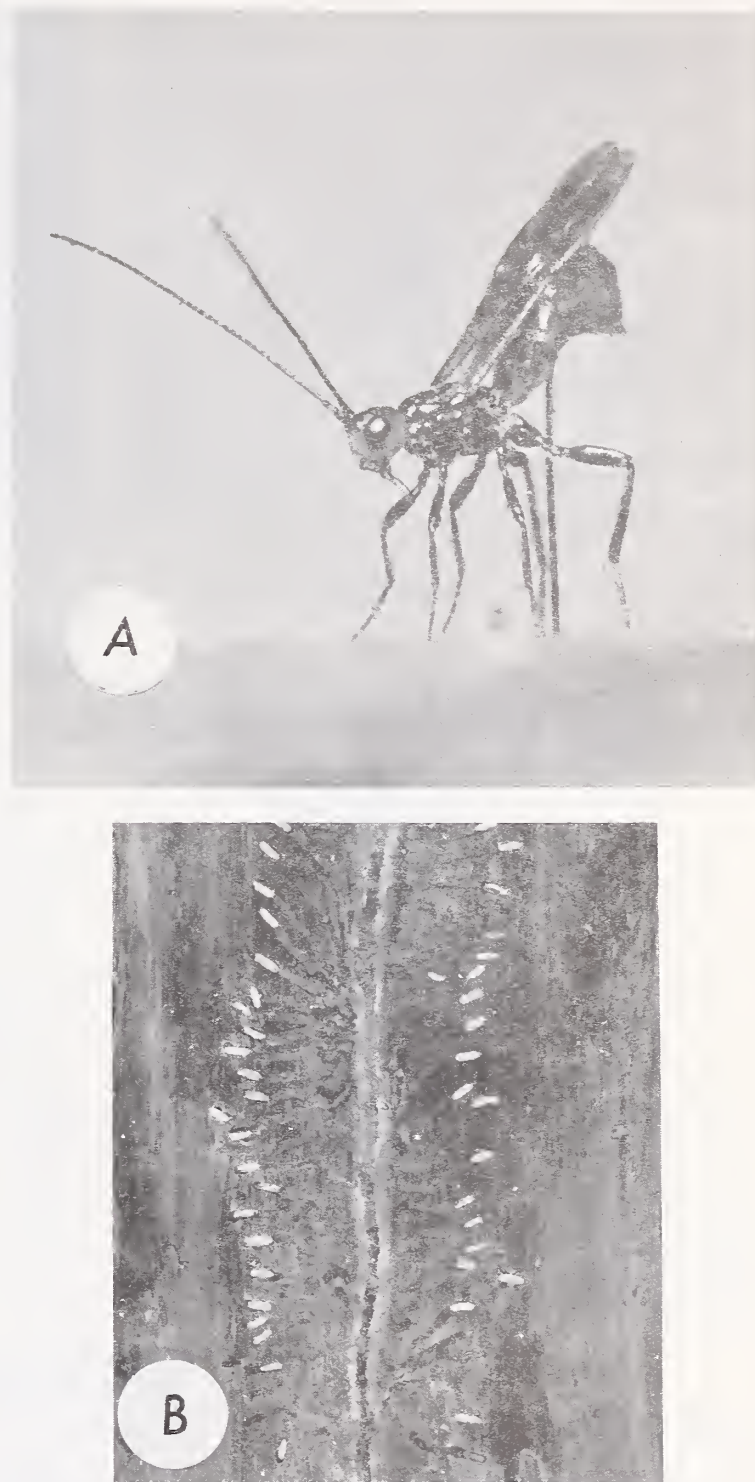


Figure 4.--*Coeloides vancouverensis* ovipositing (A) on beetle larva in bark, and cocoons (B) marking demise of beetle larvae.

MEDETERA SPP.

Both *Medetera aldrichii* Wheeler and *M. vidua* Wh. were present, but the latter was much less abundant. Adults (fig. 5A) began to appear in late May, becoming abundant in June. Eggs are laid on small groups of 1 to 3 in bark crevices (Bedard 1933). Larvae (fig. 5B) began to appear on samples June 30. The average number of Douglas-fir beetle larvae killed per *Medetera* larva is unknown.



Figure 5.--*Medetera* adult (A) and larva (B).



ENOCLERUS SPHEGEUS Fab.

Enoclerus sphegeus Fab. adults (fig. 6A) emerged in May and preyed on attacking adult Douglas-fir beetles. Eggs are laid in clusters under scales of the outer bark (Kline and Rudinsky 1964). The newly hatched larvae apparently enter the beetle galleries through holes made by the bark beetles, after which they feed on immature stages of *D. pseudotsugae*.

Larvae of *E. sphegeus* (fig. 6B) were present on samples throughout the sampling period (fig. 7) although they diminished in abundance after mid-July when most larvae migrated to the root crown where they formed pupal cells in the outer bark or duff. In laboratory tests, larvae ate an average of 0.5 *D. pseudotsugae* larva per day (Bedard 1933) and 15 to 38 *Dendroctonus ponderosae* Hopk larvae, depending on prey size (Amman 1970). Such high mortality rates seem unlikely in nature due to the somewhat dispersed and isolated nature of prey larvae.



Figure 6.--Two predators of similar habit: *Enoclerus sphegeus* adult (A) and larva (B); and *Temnochila chlorodia* adult (C) and larva (D) searching for prey.

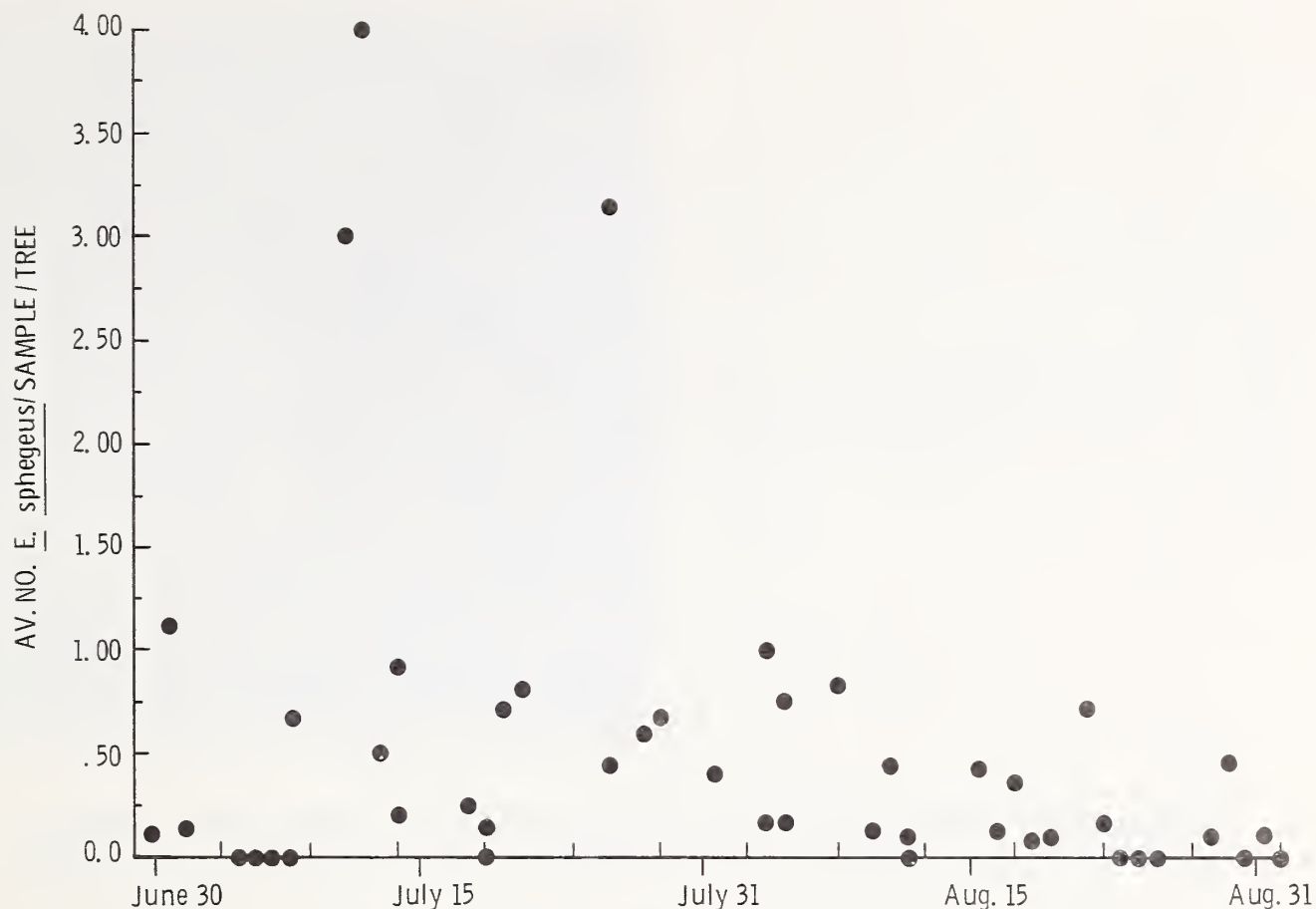


Figure 7.--Average number of *Enoclerus sphegeus* per sample per tree by day of the year on which the tree sampled.

THANASIMUS UNDATULUS Say

Larvae of *Thanasimus undatulus* Say were present at low frequency (fig. 8). They may prefer smaller bark beetles such as *Pseudohylesinus nebulosus* (Lec.) or *Scolytus monticolae* (Sw.) (Schmitz 1978). The seasonal history is similar to that of *E. sphegeus* with the exception that the larvae do not migrate to the base of the tree.

TEMNOCHILA CHLORODIA [Mann.]

T. chlorodia larvae (fig. 6D) were found throughout the summer in abundance similar to the clerids (fig. 9). More recent work indicates that this metallic green or blue predator (fig. 6C) is much less abundant in northern Idaho (Furniss and others 1979). It also seems less important in Douglas-fir of western Oregon (Kline and Rudinsky 1964). The seasonal history of *T. chlorodia* follows that of *E. sphegeus* except that the larvae do not migrate.

ROPTROCERUS ECCOPTOGASTERI Ratz, *CECIDOSTIBA BURKEI* Crawford, and *CECIDOSTIBA DENDROCTONI* Ashmead

These pteromalids are grouped together because the larvae (fig. 10) are similar in appearance and habit. They may be more important as parasites of *Pseudohylesinus nebulosus* [Lec.] and *Scolytus monticolae* [Sw.] in tops of trees killed by *D. pseudotsugae*. These parasites were most abundant in the late summer (fig. 11).

BELOSTA ALBIPILOSA Hardy

The scenopinid fly, *B. albipilosa* [Hardy] (fig. 12) was discovered in this study for the first time preying on Douglas-fir beetle progeny beneath bark (Kelsey 1969, p. 275). The segmented white larvae are elongate and possess a beak-like extension of the head (fig. 12). They were recorded on samples only in late summer (fig. 13).

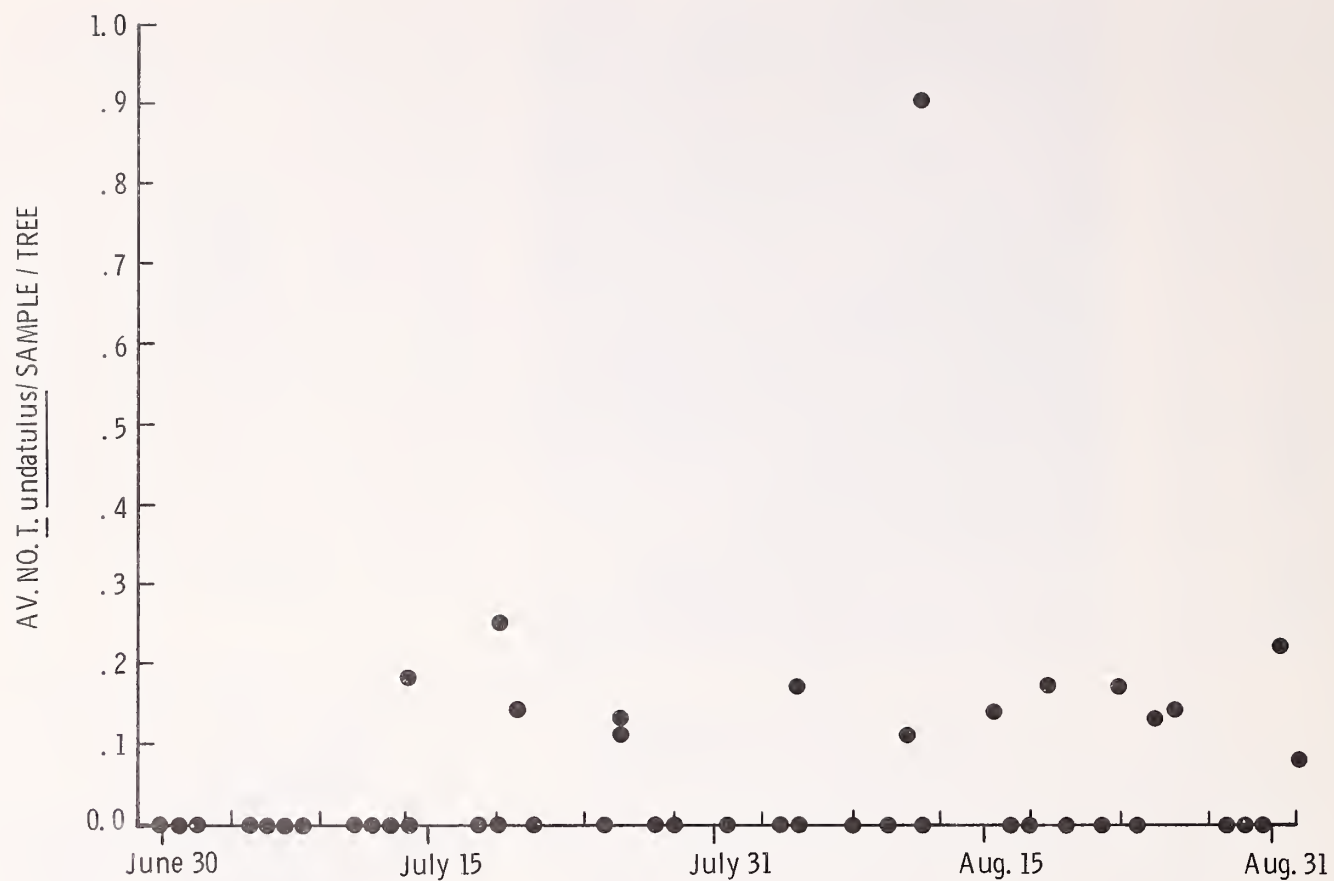


Figure 8.--Average number of *Thanasimus undatulus* per sample per tree by day of the year on which the tree was sampled.

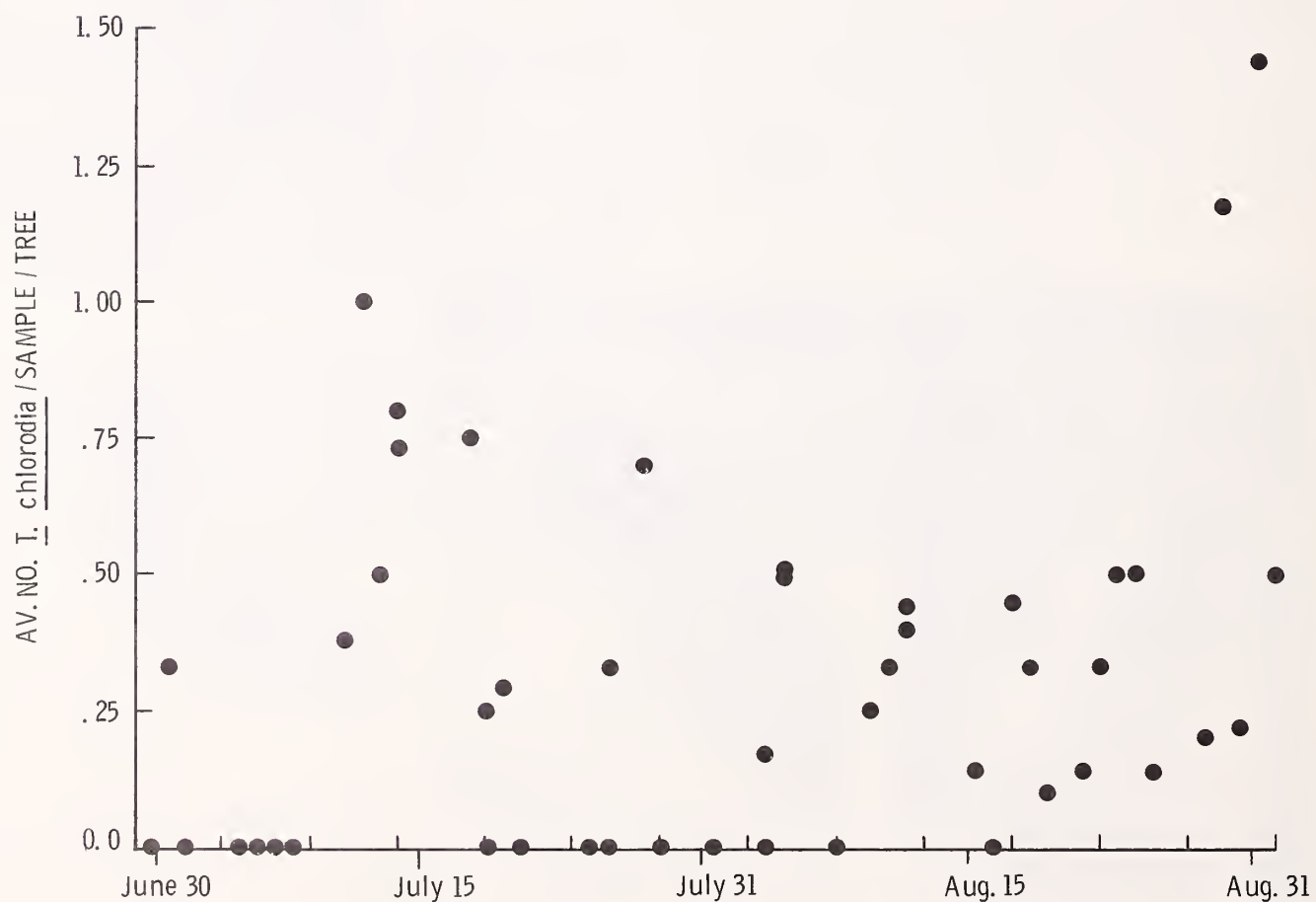


Figure 9.--Average number of *Temnochila chlorodia* per sample per tree by day of the year on which the tree was sampled.



Figure 10.--*Roptrocerus* larva recognizable by crescent shape and absence of cocoon.

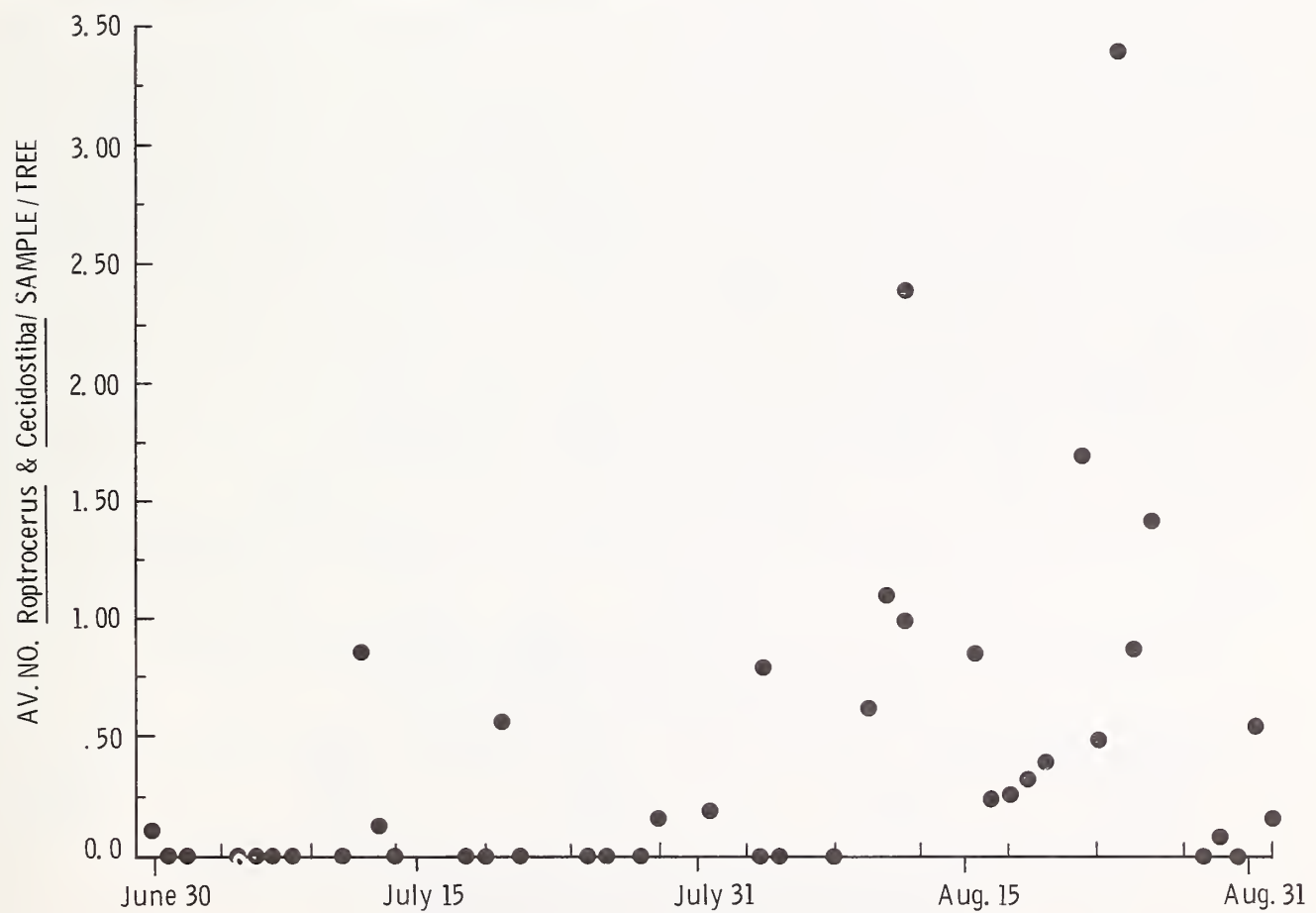


Figure 11.--Average number of *Roptrocerus* and *Cecidostiba* per sample per tree by day of the year on which the tree was sampled.



Figure 12.--*Belosta albipilosa* adult (A) and larva (B). The snakelike larva was discovered as a predator of Douglas-fir beetle during this study.

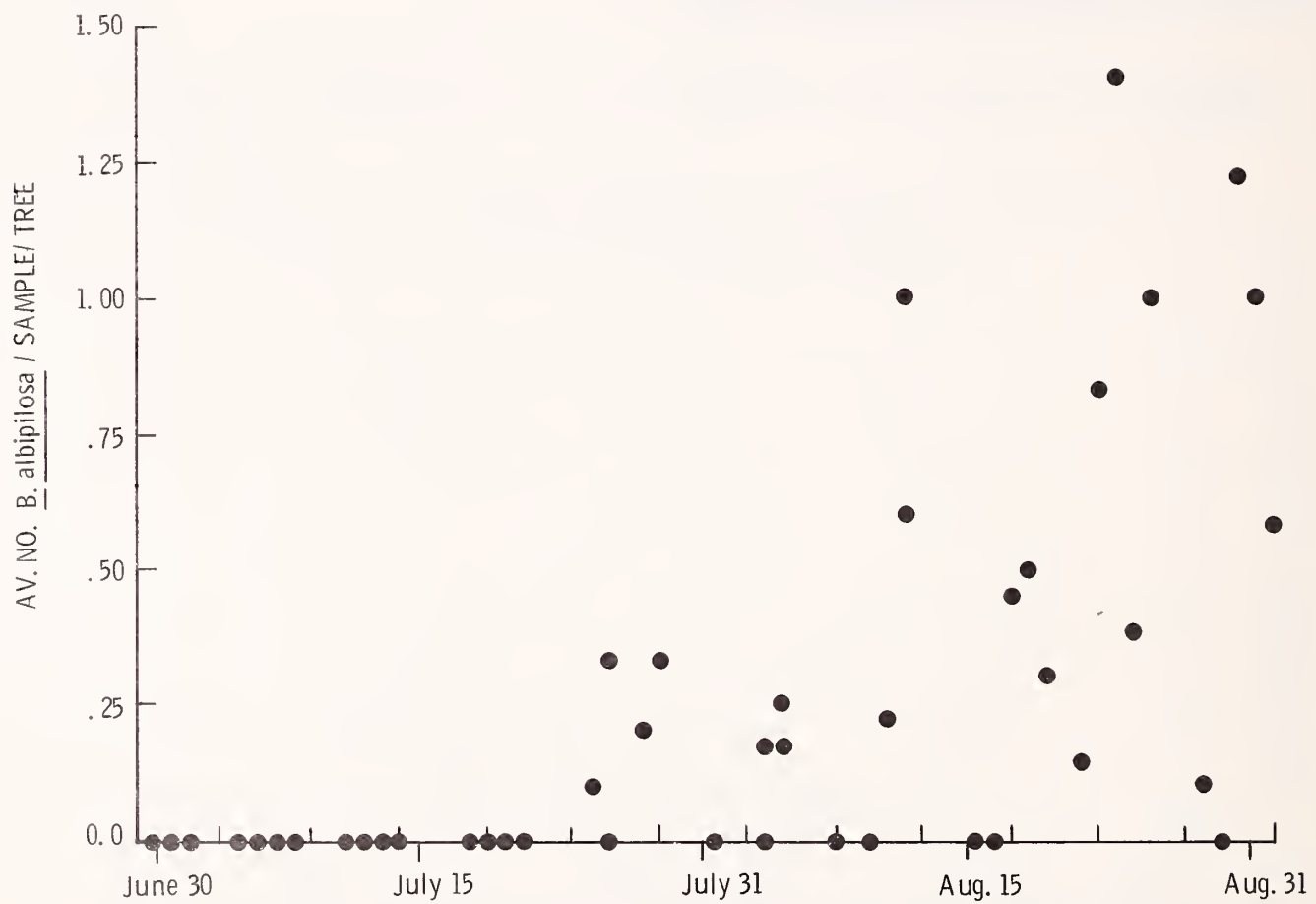


Figure 13.--Average number of *Belosta albipilosa* per sample per tree by day of the year on which the tree was sampled.

RESULTS AND DISCUSSION

After June 20, the length of egg galleries per tree did not increase. Therefore, if it were not for mortality factors the beetle population would have remained constant through the summer; however, density of beetle progeny per sample declined (fig. 14).

We hypothesize that the principal cause of reduction in beetle numbers in a **successfully** infested tree was due to entomophagous insects, not tree resistance or competition among progeny. This premise is supported by the following facts. We sampled only successfully attacked trees, that is, those low in resistance. Mortality from predation and parasitism acted to thin out progeny, lessening competition. The presence of the braconid wasp, *Coeloides*

vancouverensis [Dalla Torre] (= *brunneri* Vier.) coincided with a sudden reduction in the beetle population. The average number of Douglas-fir beetle progeny was 4.72 per decimeter of egg gallery per tree. For sample trees with low numbers of entomophagous insects the average number of beetle progeny was 11.26 per dm of egg gallery. The ratio was 32.48 for the only tree lacking entomophagous insects when sampled.

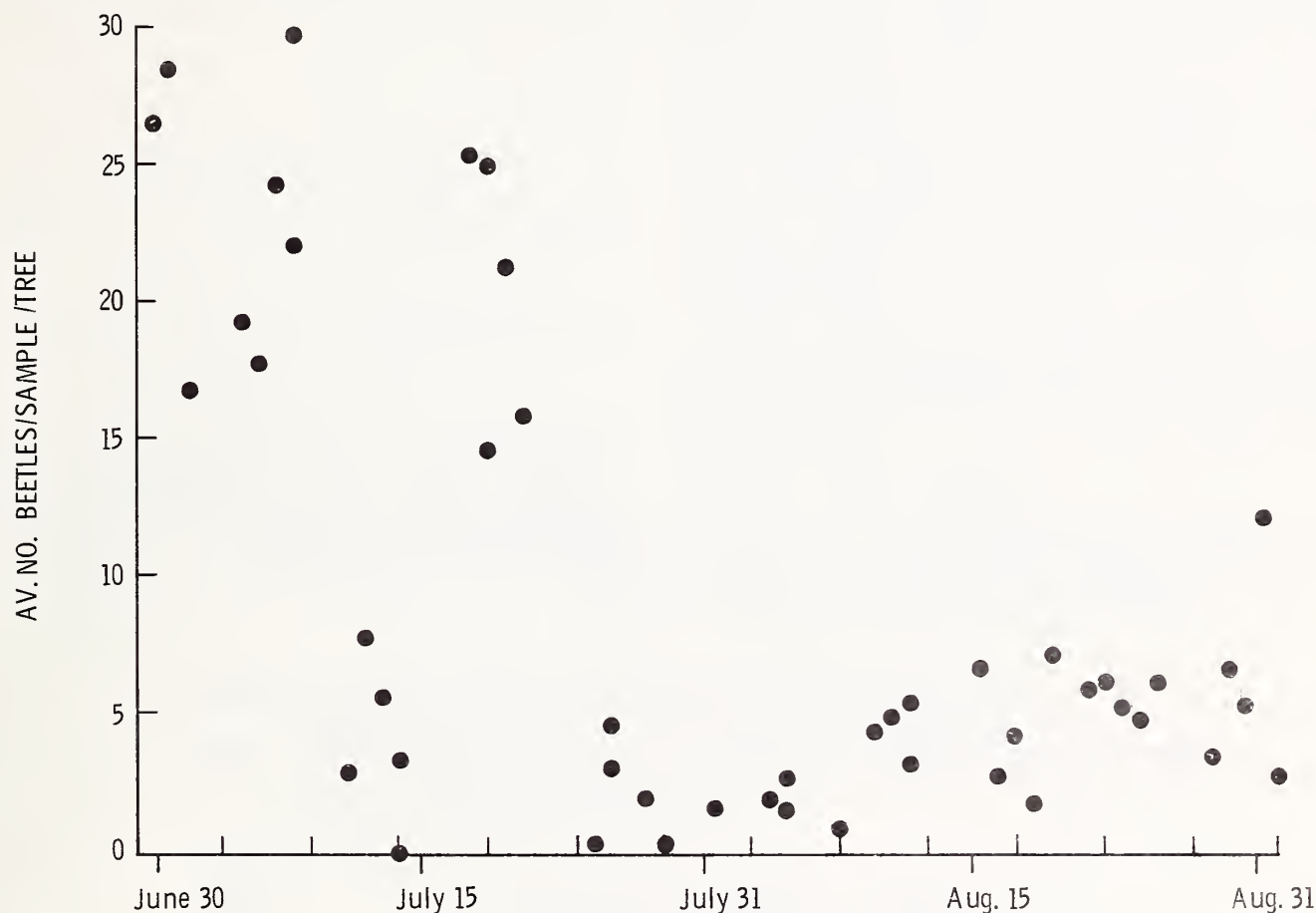


Figure 14.--Average number of Douglas-fir beetles per sample per tree by day of the year on which the tree was sampled.

Although the length of egg galleries did not increase on samples through the summer, it varied greatly from tree to tree. To remove most of this variation, we plotted over time the number of beetles per average length of egg gallery (fig. 15).

As expected, the number of Douglas-fir beetle progeny

were inversely related to numbers of entomophagous insects (fig. 16). Density of beetle progeny at low numbers of any observed enemies was 11.26/dm of egg gallery but only 2.76/dm (76 percent fewer) at high frequency of parasites and predators. Progeny averaged 4.72/dm (58 percent fewer).

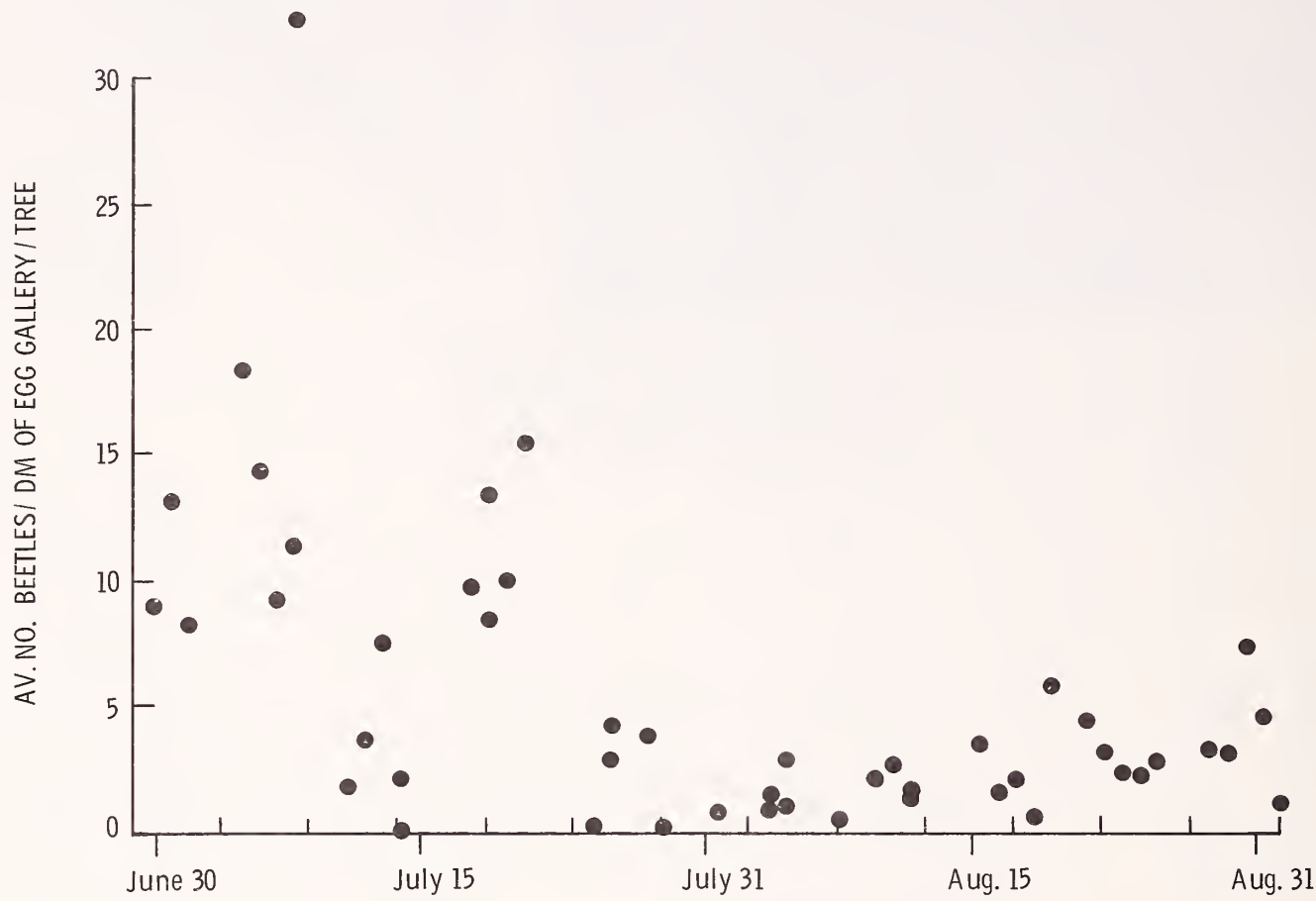


Figure 15.--Average number of Douglas-fir beetles per dm of egg gallery per tree by day of the year on which the tree was sampled.

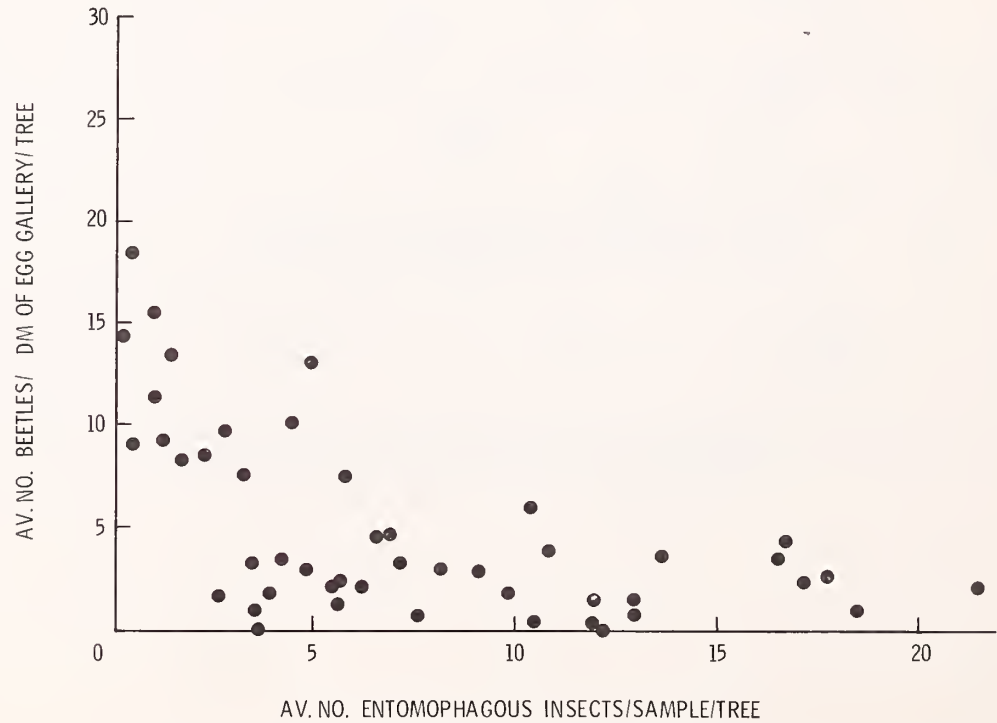


Figure 16.--Average number of Douglas-fir beetles per dm of egg gallery per tree vs. average number of entomophagous insects per sample per tree.

Population Models

DOUGLAS-FIR BEETLES

As a beginning point we used simple linear regression analysis to answer the question: Is the length of egg gallery per sample a function of tree diameter, sample height, and maximum bark thickness?

Five trees were selected at random from each of five diameter breast height classes (table 1). A quadratic effect of maximum bark thickness is suggested by these data, the average length of egg galleries being greatest at a maximum bark thickness of 1.27 to 1.78 cm. A quadratic form is also used for the sample height in the regression model:

$$Y_i = b_0 + b_1 x_{1i} + b_2 x_{2i} + b_3 x_{2i}^2 + b_4 x_{3i} + b_5 x_{3i}^2 + e_i$$

where:

- Y_i = length of egg gallery in the i th sample,
- x_{1i} = diameter at 1.5 m of tree from which i th sample is taken,
- x_{2i} = maximum bark thickness for the i th sample,
- x_{3i} = height at which i th sample occurred on the tree,
- e_i = error associated with i th sample,

This regression model was then fitted to the total data set.

The regression model accounted for only a small percentage of the variation in the average length of egg galleries as indicated by the multiple correlation coefficient, $R^2 = 0.111$. The regression coefficient/significance levels were:

$$\begin{aligned} b_0 &= 6.685/0.001 & b_4 &= 0.0818/.054 \\ b_1 &= -0.1109/.015 & b_5 &= 0.008/.047 \\ b_2 &= -1.192/0.485 \\ b_3 &= 0.2691/0.627 \end{aligned}$$

The significant coefficients in the model, i.e., those statistically different from zero, are tree diameter and sample height. The coefficients for maximum bark thickness were not different from zero.

Thus, for sampling length of egg galleries (which are proportional to initial beetle population), we conclude that tree diameter and sample height, not bark thickness, need be considered. As we discuss later, however, mortality factors such as *C. vancouverensis* are affected by bark thickness.

In sampling Douglas-fir beetles it is less costly to take samples from the more accessible lower part of standing trees. Would this result in a biased estimate of the density of bark beetles? In table 2 the density at 1.5 m is about one-half the average tree density. The density at 4.6 m is very close to the average density of egg galleries, and the simple correlation of the 4.6 m sample with the tree average is $R_{yx} = 0.640$, ($R_{yx}^2 = 0.410$). Therefore, average Douglas-fir beetle attack density per tree is estimated better at the 4.6 m height (a slightly lower height may suffice [Furniss 1962b]).

In order to relate 4.6 m samples to the tree as a whole, however, one needs a regression estimator (Kish 1965). From a regression of the average beetle density per tree on the density at the 4.6 m level, the following relationship was obtained:

$$Y_i = 0.750 + 0.580 X_i,$$

where Y_i is average beetle density in the tree, X_i is the beetle density in the 4.6 m level sample.

Table 1.--Length of egg galleries (dm) and maximum bark thickness (cm) by sample height (m) for 5 sample trees in each of 5 diameter classes. The diameter (cm) for each tree at 1.5 m height is also presented

Sample height (m)	Average diameter (cm) at 1.5 m height				
	27.9	43.2	63.5	71.1	81.3
32.0					1.27(2.06)
29.0					1.02(0.48)
25.9					1.27(0.25)
22.9			1.02(2.46)	1.52(1.37)	1.78(3.53)
19.8			1.02(2.29)	1.27(2.34)	1.52(1.07)
16.8			1.02(2.79)	1.78(2.64)	1.78(0.81)
13.7		0.76(0.0)	1.52(2.34)	1.78(2.54)	2.29(2.01)
10.7		1.02(1.80)	1.27(2.41)	2.29(1.80)	2.03(3.00)
7.6	1.02(0.0) ¹	1.27(3.23)	2.03(1.45)	2.03(1.45)	2.29(1.32)
4.6	1.02(.91)	1.52(1.73)	1.78(1.68)	3.30(1.32)	2.54(1.32)
1.5	1.27(1.40)	2.79(0.0)	3.30(0.76)	5.08(0.0)	5.59(1.78)

¹Maximum bark thickness (cm) and (length of egg galleries (dm)).

Table 2.--Average and variance of length of Douglas-fir beetle egg galleries/sample per tree at the two lowest heights

Height	Length of galleries (dm)	Variance
1.5 m	0.81	0.68
4.6 m	1.60	.57
Average for tree	1.67	.46

Predators and Parasites

Sampling the Douglas-fir trees at the 4.6 m height may provide useful estimates of the density of bark beetles per tree, but what of predator and parasite densities?

Table 3 shows that for some predators and parasites (including the two most abundant) the 4.6 m sample is not a good estimate of the average density per tree. For *C. vancouverensis* the 4.6 m sample greatly underestimates the population (all-tree sample) density. For *Medetera* spp. the 4.6 m sample overestimates the all-tree sample by a large amount. *Roptrocercus* sp. and *Cecidostiba* sp. also have much larger densities per tree based on all samples than the density based on 4.6 m samples. However, these last two occur in very low frequency and are probably mainly parasites of other (secondary) bark beetles high in the tree.

Because *C. vancouverensis* and *Medetera* spp. were the most abundant parasite and predator, their distributions on the tree will be evaluated further.

Table 3.--Average number of predators and parasites per sample per tree and per sample at 4.6 m height

Species	Number per sample per tree	Number per sample at 4.6 m height
<i>Enoclerus sphegeus</i>	0.4973	0.5833
<i>Thanasimus undatulus</i>	.0699	.0416
<i>Temnochila chlorodia</i>	.3333	.4375
<i>Coeloides vancouverensis</i>	3.4919	1.7500
<i>Roptrocercus</i> sp. and <i>Cecidostiba</i> sp.	.4274	.2083
<i>Medetera</i> spp.	2.1693	3.5000
Total	7.4462	6.9375

COELOIDES VANCOUVERENSIS

Of the 372 samples taken, 80 contained *C. vancouverensis*. Of the 48 trees sampled, 21 contained *C. vancouverensis*. One hundred and twenty-three *C. vancouverensis* were found on samples in one tree and 50 occurred on one sample. This indicates a contagious distribution. We herein explore some reasons for this distribution.

Coeloides vancouverensis deposits eggs singly through the bark onto a 2nd, 3rd, or 4th instar *D. pseudotsugae* larva (Ryan and Rudinsky 1962). Larvae of this parasite were found beginning July 12, 12 days after start of sampling. The female is excluded from ovipositing in those areas of the tree where overlying bark is thicker than the 5 mm length of her ovipositor. Density and distribution of host larvae, also govern the location and abundance of *C. vancouverensis*.

To model the distribution of *C. vancouverensis* at a sample location, a logistic function was chosen. The response variable (Y) was recorded as 1 if the parasite was present; 0 if the absent on a sample. The logistic function which defines the probability of the presence of a given insect is given by $Y = P(n > 0) = (1 + \text{EXP}[-BX])^{-1}$, where n is the number of *C. vancouverensis* (an integer greater than or equal to zero). EXP is the exponential function. X is a vector of independent variables (bark thickness, height, etc.). B is a vector of coefficients to be estimated.

Walker and Duncan (1967) developed an efficient method of estimation for the coefficient vector B . The algorithm has been packaged as a computer program in Fortran IV (Hamilton 1974). Using that procedure, the following model was derived for individual samples:

$$Y_j = (1 + \text{EXP}[f(X_j, B)])^{-1} + e_j$$

where

$$f(X_j, B) = B_0 + B_1 X_{1j} + B_2 X_{2j} + B_3 X_{3j} + B_4 X_{4j}$$

and e_j is the error associated with the j th sample.

The variables used have the following identification:

- Y_j = the presence of *C. vancouverensis* (1 = present, 0 = absent),
- X_{1j} = date of the j th sample,
- X_{2j} = length of egg galleries (dm) in the j th sample,
- X_{3j} = maximum bark thickness (cm) of the j th sample,
- X_{4j} = number of ventilation holes in the j th sample,

The estimates of these coefficients based on this data set are:

$$\begin{aligned} b_0 &= -13.6380 & b_3 &= -0.6450 \\ b_1 &= 0.0650 & b_4 &= 0.1680 \\ b_2 &= 0.1299 \end{aligned}$$

The degree of fit is seen in table 4. Here the observations are grouped into classes according to their predicted values. For example, Class 1 contains only one observation. Of the 372 samples, the model predicted a probability of 0.01 or less *C. vancouverensis* for only one sample. This sample did not contain *C. vancouverensis*. By contrast, Class 20 contains those samples for which the predicted probability of containing *C. vancouverensis* is $0.90 < 0.95$. This class contains 10 samples of which 9 contain *C. vancouverensis*. The excellent agreement of expected and observed *C. vancouverensis* is indicated by a chi-square statistic of 0.01 for this class. An overall chi-square for the 21 classes is 13.60, which indicates good degree of fit for the logistic function.

Table 4.--Number of samples with *C. vancouverensis* as a function of the expected frequency and chi-square values for degree of agreement between the expected and observed frequencies

Class	Probability of presence of <i>C. vancouverensis</i>	Number of samples	Number of samples with <i>C. vancouverensis</i>	Expected number of samples with <i>C. vancouverensis</i>	Chi-square
1	0.0 - 0.01	1	0	0.0	0.01
2	.01 - .05	9	0	.3	.27
3	.05 - .10	23	0	1.7	1.73
4	.10 - .15	35	1	4.4	2.63
5	.15 - .20	33	4	5.8	.55
6	.20 - .25	27	6	6.1	.00
7	.25 - .30	21	8	5.8	.87
8	.30 - .35	19	11	6.2	3.83
9	.35 - .40	14	7	5.2	.59
10	.40 - .45	9	2	3.8	.88
11	.45 - .50	8	5	3.8	.38
12	.50 - .55	5	2	2.6	.15
13	.55 - .60	18	13	10.3	.70
14	.60 - .65	15	11	9.4	.29
15	.65 - .70	20	14	13.5	.02
16	.70 - .75	18	12	13.0	.09
17	.75 - .80	30	21	23.2	.23
18	.80 - .85	34	29	28.0	.03
19	.85 - .90	18	14	15.7	.20
20	.90 - .95	10	9	9.2	.01
21	.95 - 1.00	5	4	4.9	.16
Total					13.60

Figure 17 shows the relationship of date and the probability of *C. vancouverensis* being present, if other variables in the model are held at their average values. This function reflects the rapid increase in frequency of *C. vancouverensis* during midsummer (fig. 18). The probability of presence of *C. vancouverensis* is also positively correlated with the average length of egg galleries (fig. 19). Bark thickness strongly affects the probability of occurrence of *C. vancouverensis* (fig. 20). Samples at 4.6 m height contain thicker bark than samples taken higher up the tree, and this explains why the 4.6 m sample under estimates the average density of *C. vancouverensis*.

MEDETERA SPP.

Medetera spp. were the most numerous predators in the trees and occurred over the entire sampling time period (fig. 21). They were found more frequently at the 4.6 m level than on the average of all samples from the tree. Greater moisture in thick bark portions of the tree probably protect the larvae from desiccation.

Again the logistic model can be employed to determine where the *Medetera* spp. are most likely to occur. The model is of the form:

$$Y_j = P(n_j > 0) = (1 + \text{EXP}[X_j, B])^{-1} + e_j$$

where the function $f(X_j, B)$ will contain both linear and quadratic terms and e_j is the random error component.

The following variables were used in the model:

Y_j = the presence of *Medetera* spp. (1 = present, 0 = absent),

X_{1j} = the date of the i th sample,

$X_{2j} = X_{1j}^2$,

X_{3j} = the height (m) of the i th sample,

$X_{4j} = X_{3j}^2$,

X_{5j} = the maximum bark thickness (cm) of the i th sample,

$X_{6j} = X_{5j}^2$,

X_{7j} = the number of ventilation holes in the i th sample,

$X_{8j} = X_{7j}^2$,

X_{9j} = the diameter (cm) of the tree at the height where the j th sample was taken.

The sample estimates of the coefficients for the above model are:

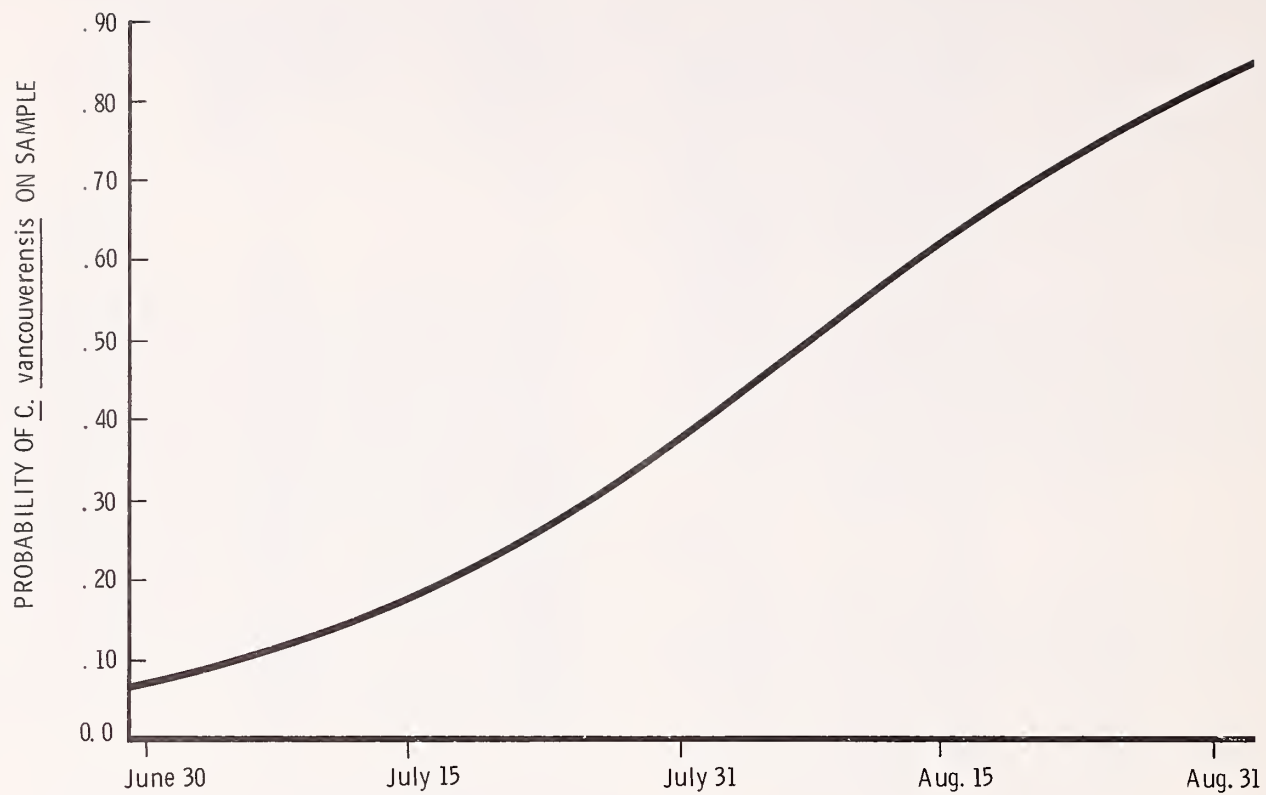


Figure 17.--Probability of *C. vancouverensis* on a sample as a function of day of the year.

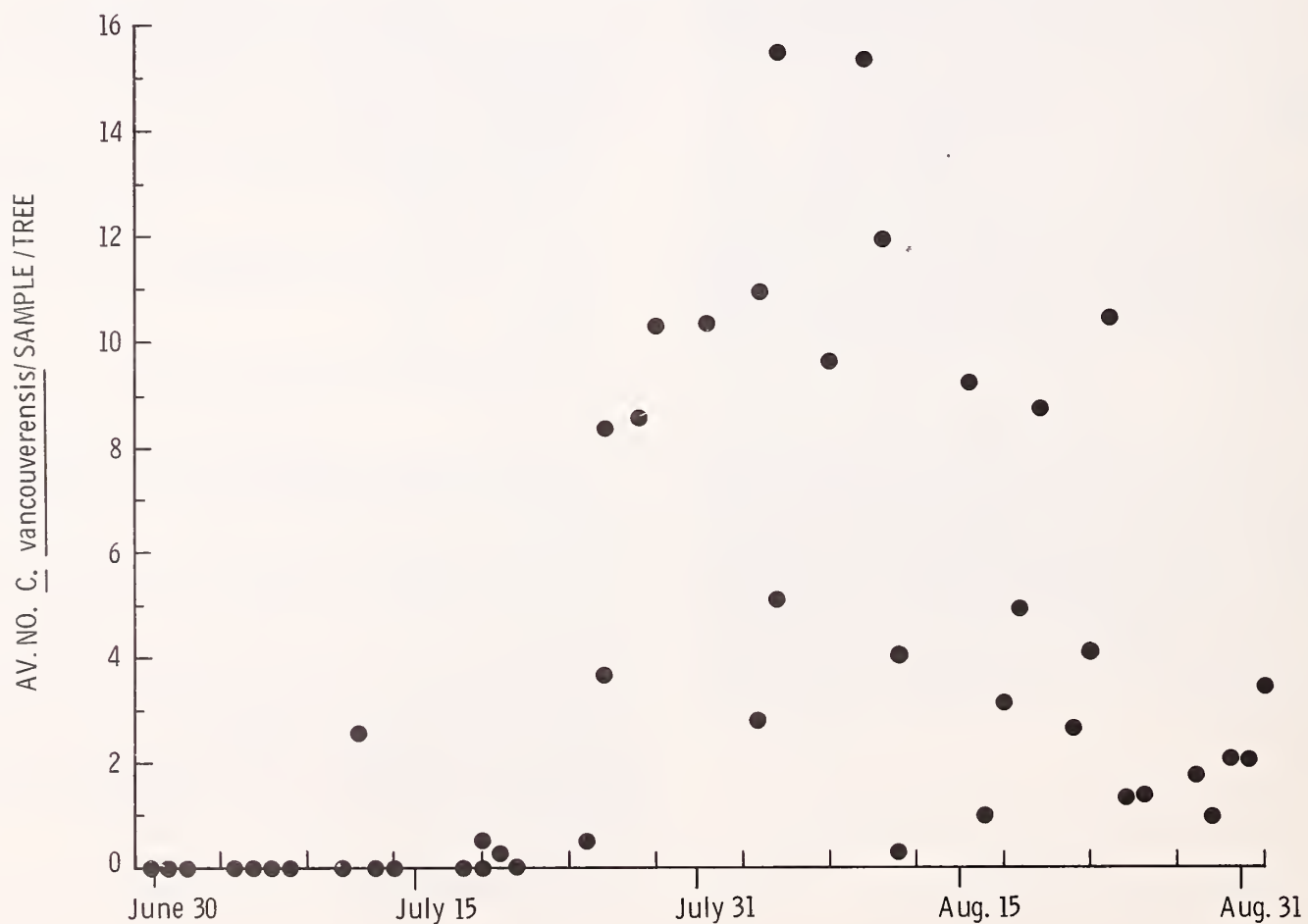


Figure 18.--Average number of *C. vancouverensis* per sample per tree by day of the year on which the tree was sampled.

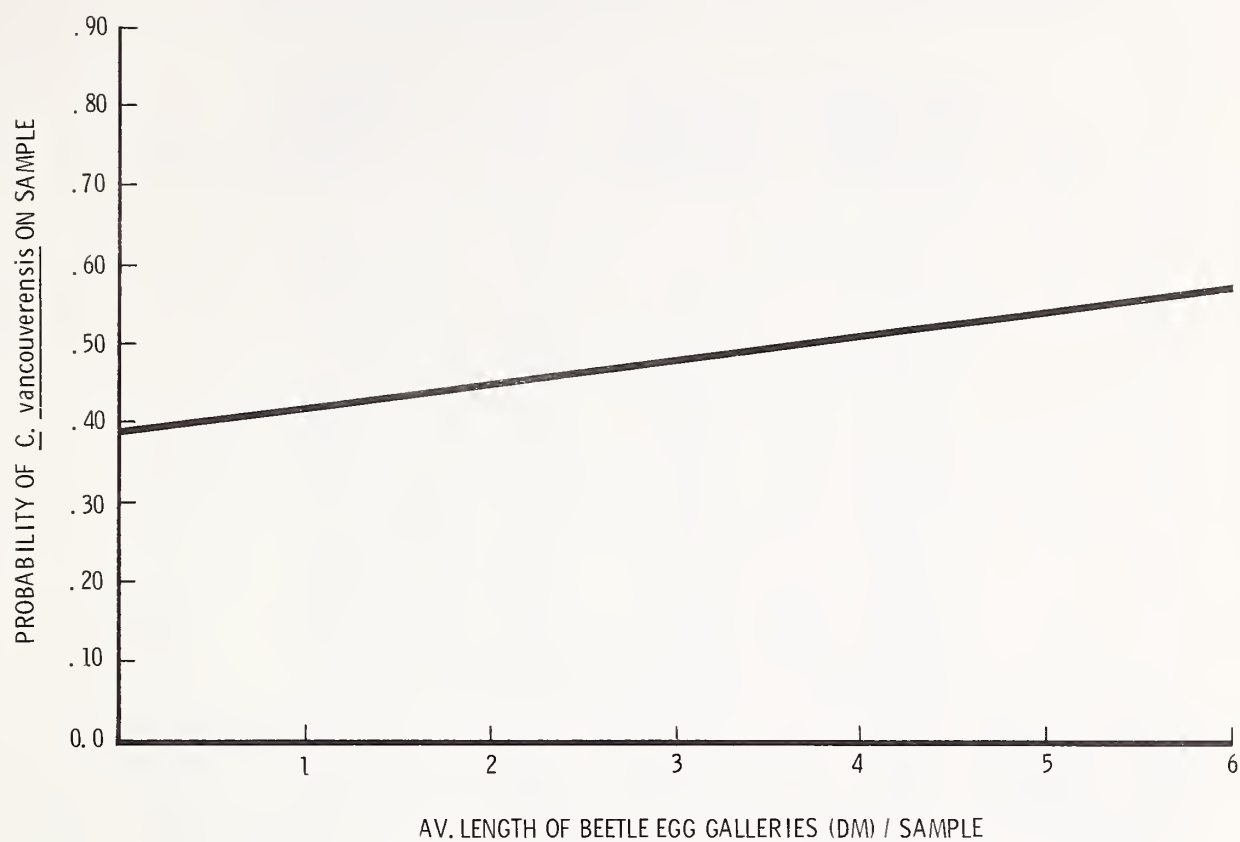


Figure 19.--Probability of *C. vancouverensis* on a sample as a function of length (dm) of Douglas-fir beetle egg galleries per sample.

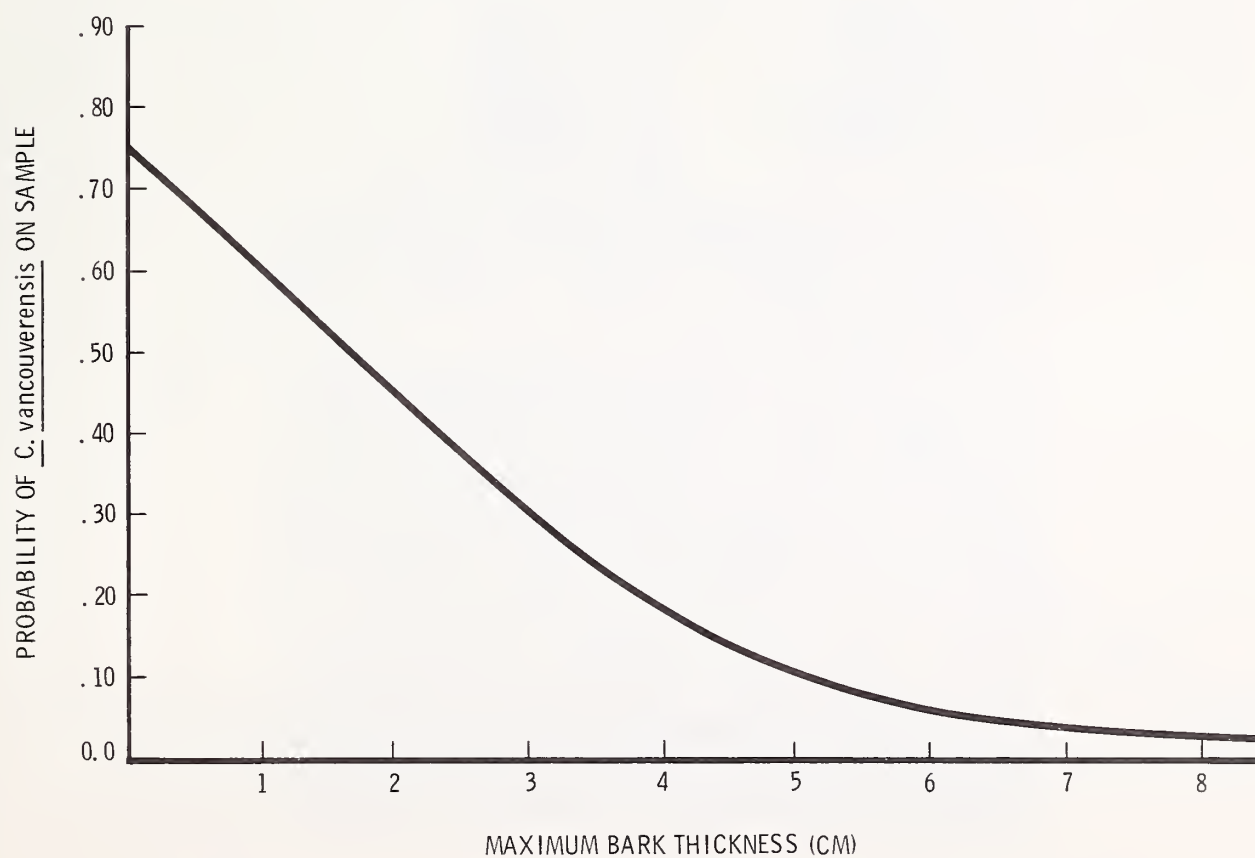


Figure 20.--Probability of *C. vancouverensis* on a sample as a function of maximum bark thickness.

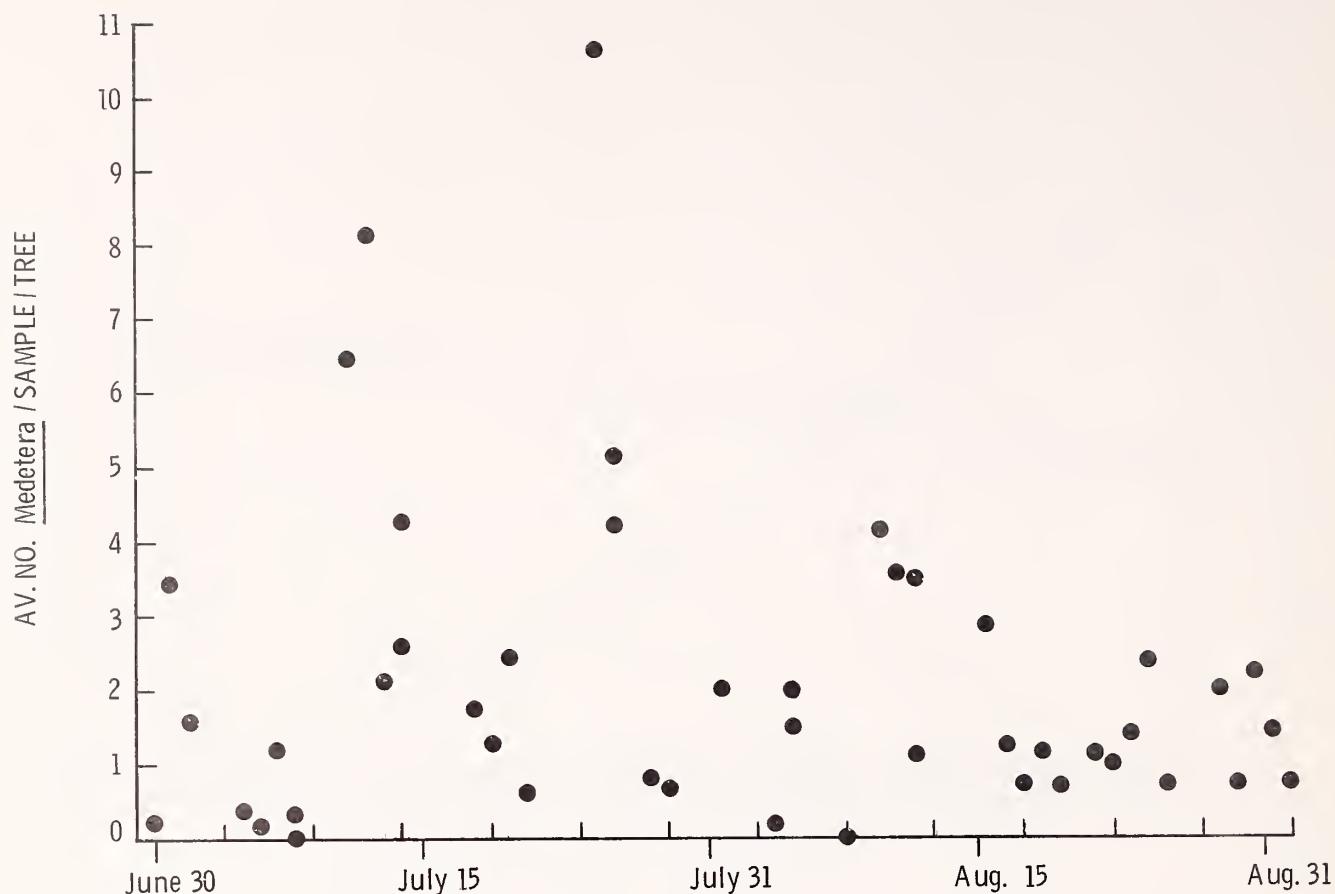


Figure 21.--Average number of *Medetera* spp. per sample per tree by day of the year on which the tree was sampled.

$$\begin{aligned}
 b_0 &= -65.0992 & b_5 &= +1.16607 \\
 b_1 &= +0.57756 & b_6 &= -0.183806 \\
 b_2 &= -0.001366 & b_7 &= +0.620687 \\
 b_3 &= +0.169242 & b_8 &= -0.057379 \\
 b_4 &= -0.0081439 & b_9 &= +0.05076
 \end{aligned}$$

The model closely fits the observed distribution of *Medetera* (chi-square 12.82, table 5). In examining the form of the model, we will discuss the sample variables individually, then jointly.

The probability of *Medetera* occurring on a sample in relation to changes in maximum bark thickness is shown in figure 22. All other variables in the model are held at their average values. The form of the curve fits our observations that *Medetera* were rare at upper heights where bark is thinner. We also know that *Medetera* were more abundant than average at the 4.6 m level. The peak of the curve occurs at about 3.25 cm, half way between the average maximum bark thickness for the 4.6 m and 1.5 m samples. The decline in abundance of *Medetera* where bark was thicker than 3.25 cm is due to the influence of 1.5 m samples (av. 3.90 cm max. bark thickness), there being fewer Douglas-fir beetle attacks and progeny at that sample height (Furniss 1962b). *Medetera* decreased in density with sample height (fig. 23) and increased with diameter (fig. 24) at the sample location.

Table 5.--Number of samples containing *Medetera spp.* as a function of the expected frequency and chi-square values for degree of agreement between the expected and observed frequencies

Class	Probability of presence of <i>Medetera spp.</i>	Number of samples	Number of samples with <i>Medetera spp.</i>	Expected number of samples with <i>Medetera spp.</i>	Chi-square
1	0.0 - 0.01	4	0	0.0	0.02
2	.01 - .05	16	1	.4	1.02
3	.05 - .10	8	2	.5	3.98
4	.10 - .15	13	4	1.6	3.45
5	.15 - .20	15	2	2.6	.13
6	.20 - .25	14	2	3.1	.41
7	.25 - .30	12	2	3.3	.51
8	.30 - .35	8	3	2.7	.05
9	.35 - .40	12	3	4.6	.56
10	.40 - .45	14	5	6.0	.16
11	.45 - .50	18	5	8.5	1.50
12	.50 - .55	27	13	14.1	.09
13	.55 - .60	20	11	11.5	.02
14	.60 - .65	30	22	18.9	.55
15	.65 - .70	27	18	18.2	.00
16	.70 - .75	33	23	23.9	.04
17	.75 - .80	37	29	28.6	.00
18	.80 - .85	25	23	20.7	.26
19	.85 - .90	24	22	20.9	.06
20	.90 - .95	14	13	12.9	.00
21	.95 - 1.00	1	1	1.0	.00
Total					12.82



Figure 22.--Probability of *Medetera spp.* on a sample as a function of maximum bark thickness.

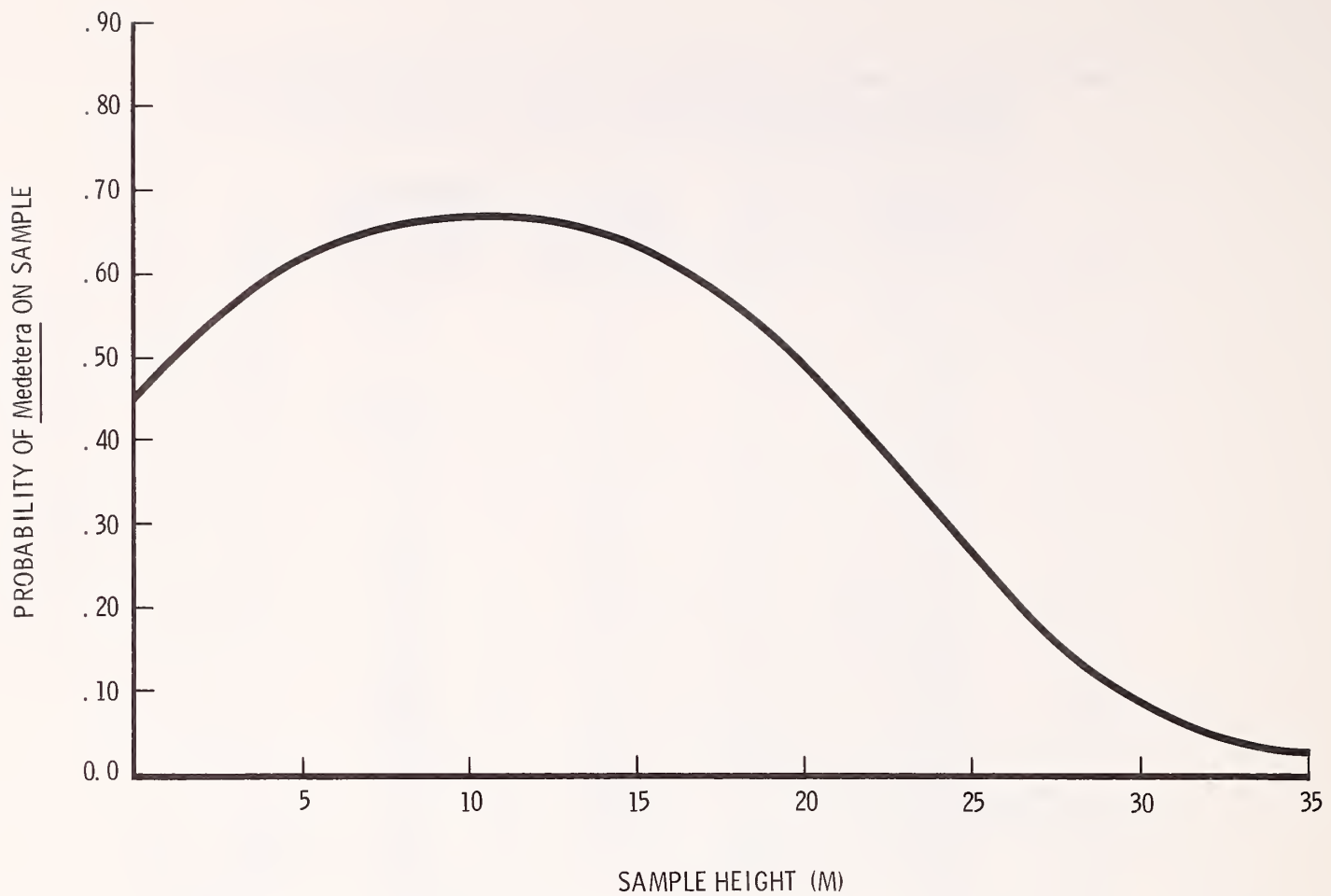


Figure 23.--Probability of *Medetera* spp. on a sample as a function of sample height.

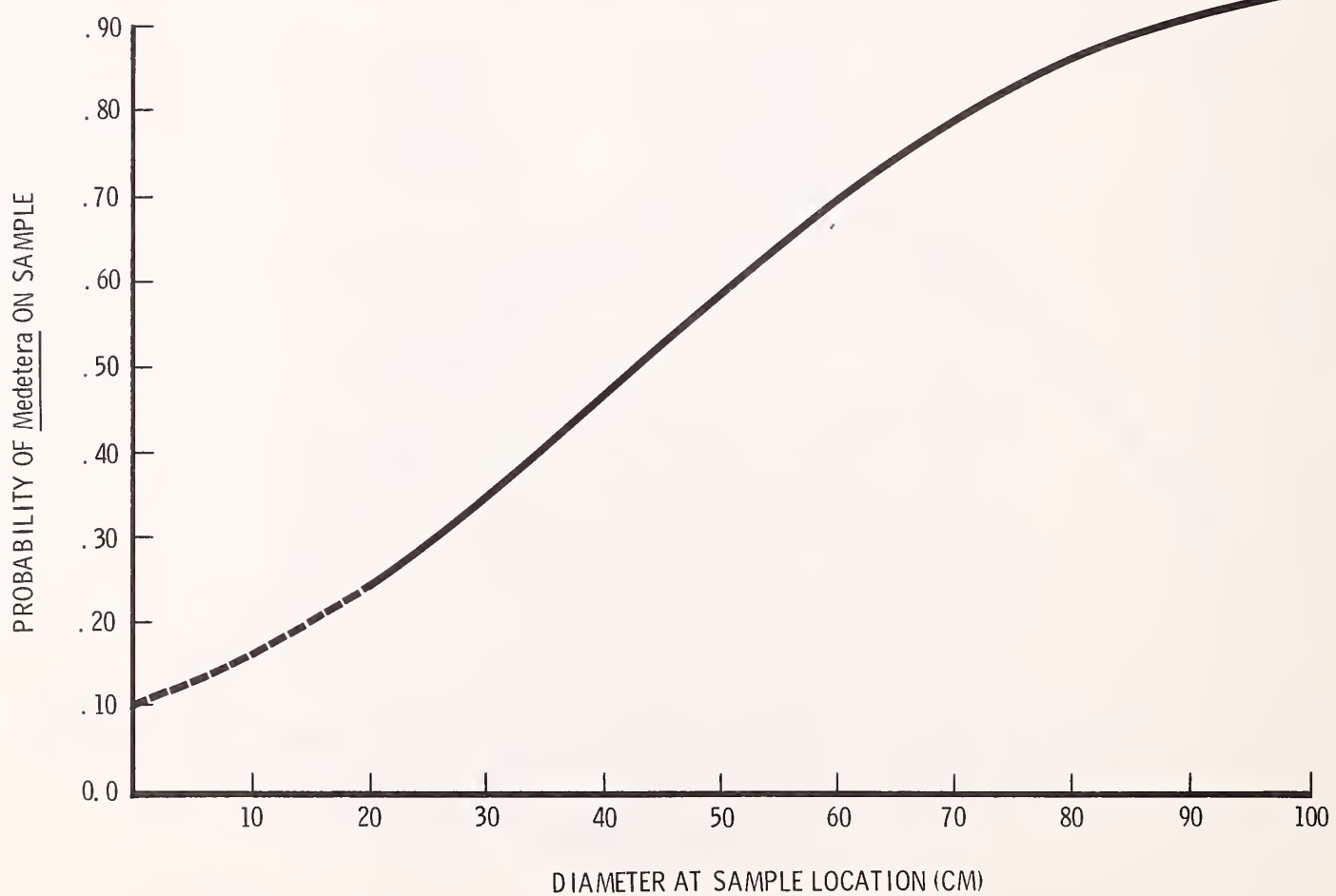


Figure 24.--Probability of *Medetera* spp. on a sample as a function of tree diameter at the sample location.

The relationship between *Medetera* and Douglas-fir beetle ventilation holes is shown in figure 25. Low numbers of ventilation holes probably indicate a low Douglas-fir beetle density and few opportunities for the predators to oviposit and to locate prey in order to survive. On the other hand, very numerous ventilation holes may have exceeded the capability of this particular *Medetera* population to exploit them as oviposition sites.

The effect of date of sample is seen in figure 26. This function may be influenced by a few trees sampled in mid-summer that had a very high density of *Medetera* spp. The subsequent decline in *Medetera*, however, might be due to drying of phloem as the season progressed, which would likely take a toll of *Medetera* larvae, especially in areas of thinner bark.

The joint effect of the physical variables that describe the sample location on a tree are seen in figure 27. Here date and number of ventilation holes are held at their average values. The diameter, maximum bark thickness, and height are values for this average tree. At heights up to 13.7 m, the probability of finding *Medetera* spp. is high (73-86 percent). As the samples are taken at heights above 14 m, the probability that *Medetera* spp. are present declines.

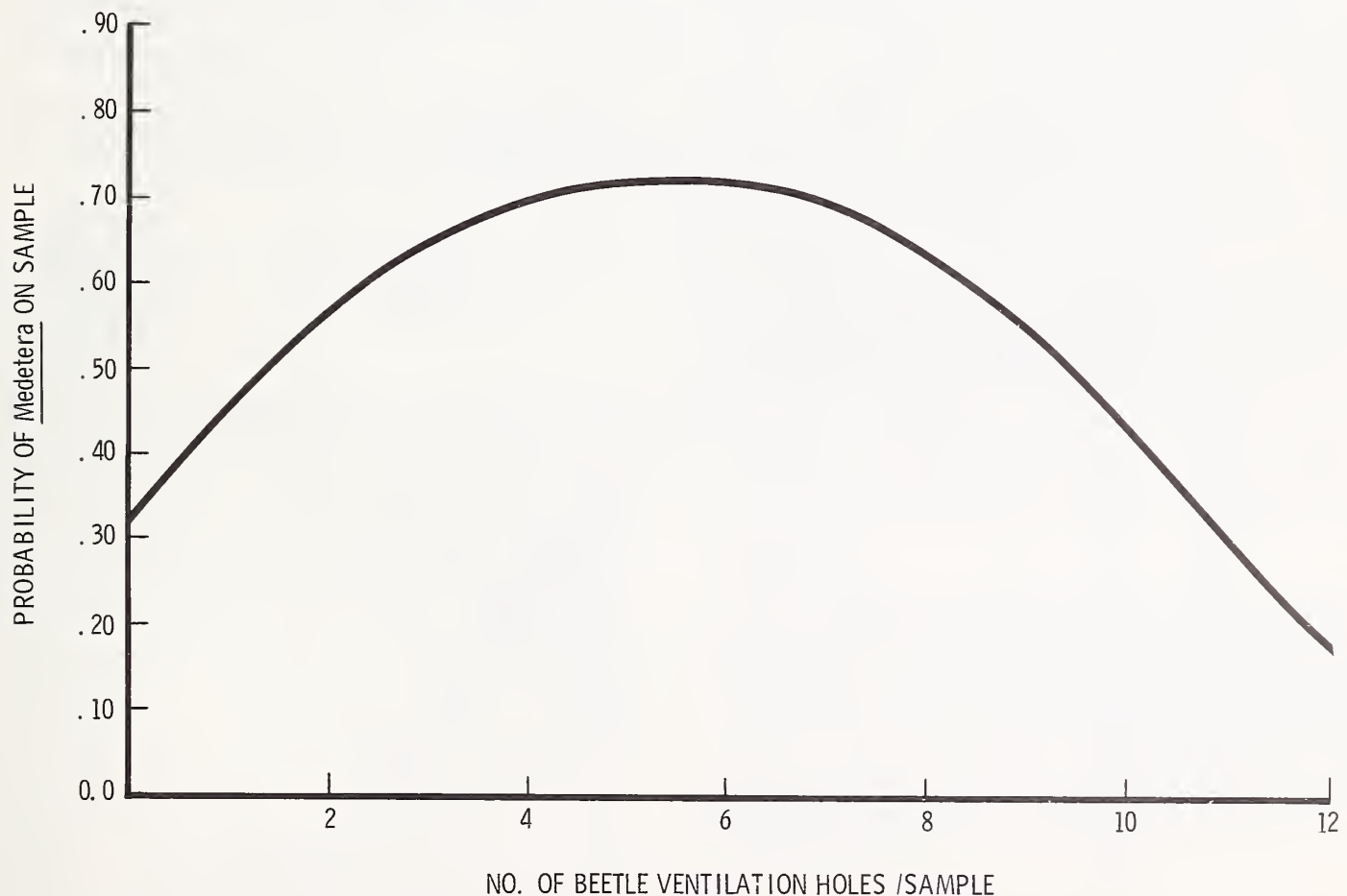


Figure 25.--Probability of *Medetera* spp. on a sample by number of Douglas-fir beetle ventilation holes per sample.

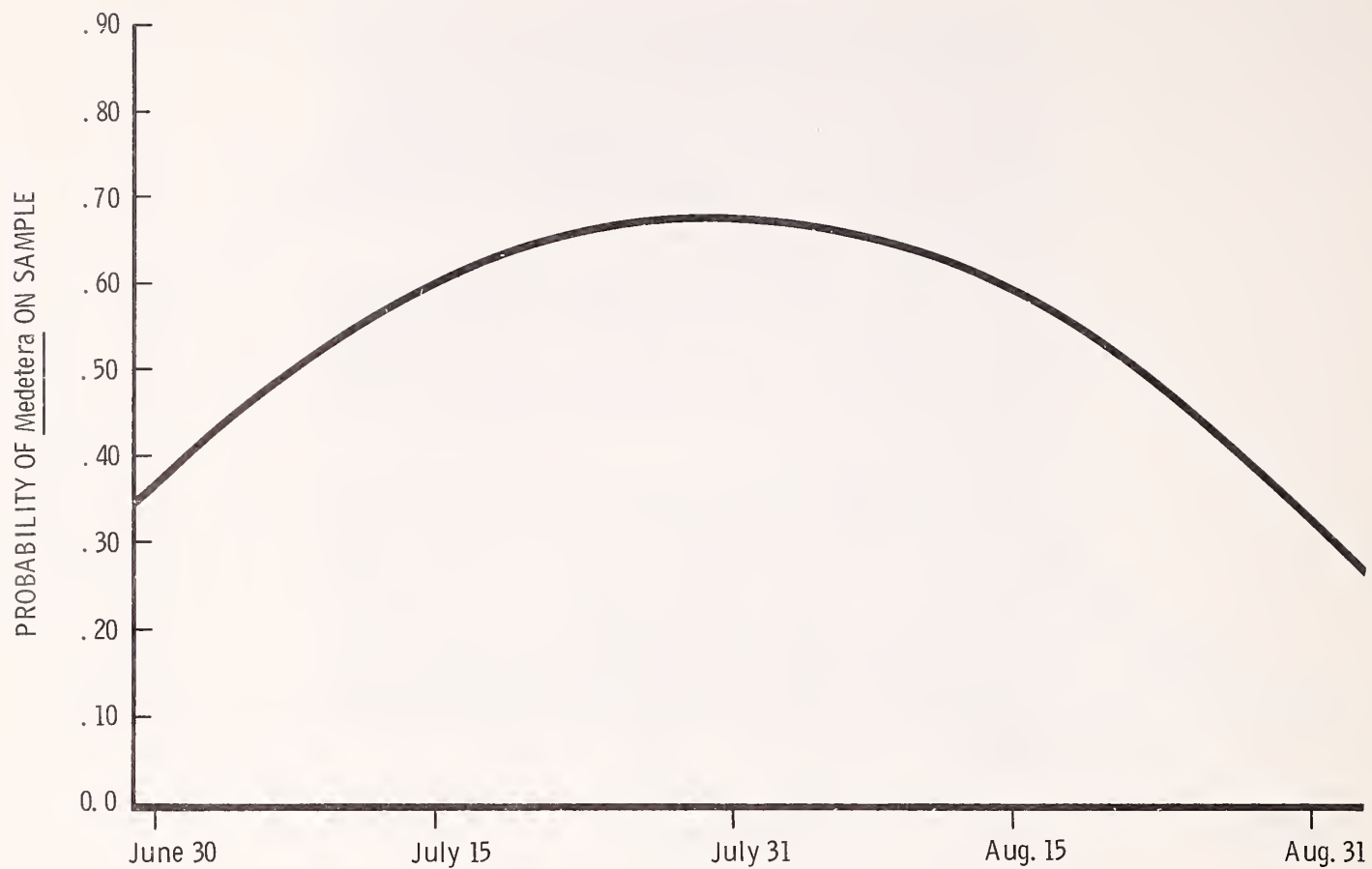


Figure 26.--Probability of *Medetera* spp. on a sample by day of the year on which the sample was taken.

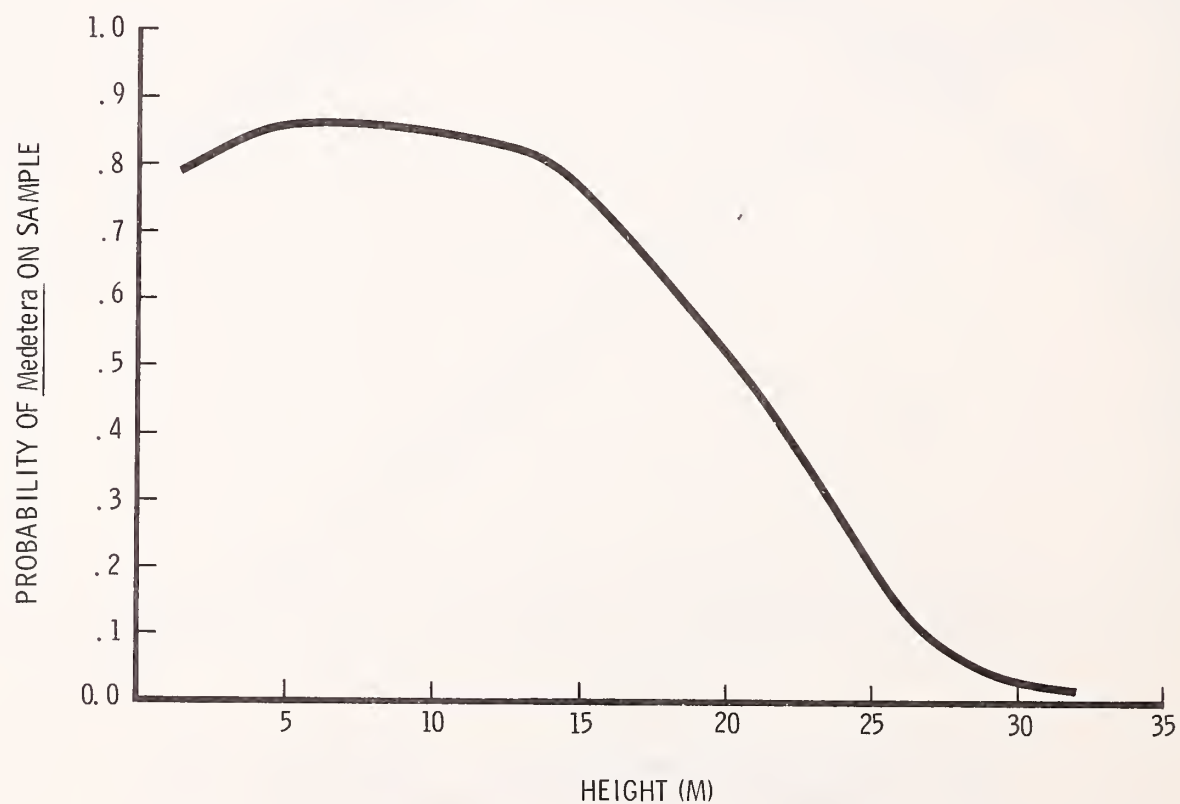


Figure 27.--Probability of *Medetera* spp. on samples on a tree using all sample variables in the prediction function.

Effect of Predators and Parasites on Douglas-fir Beetle Density

How many DFB progeny do predators and parasites kill?

Because progeny are consumed, mortality cannot be measured directly. But mortality can be estimated if the number of Douglas-fir beetles per sample is viewed as a function of length of egg gallery and number of predators and parasites. This relationship can be expressed as follows:

$$y_{ij} = B_0 + \sum_{k=1}^8 B_k X_{kij} + e_{ij}$$

Y_{ij} = number of the Douglas-fir beetle found in the j th sample of the i th tree,

X_{kij} = number of the k th predators or parasites found in the j th sample of the i th tree, ($k = 1, 2, \dots, 7$),

X_{8ij} = length of egg galleries (dm) found in the j th sample of the i th tree.

The predators and parasites are identified as follows:

$X_{1ij} = E. \text{sphegeus}$	$X_{5ij} = Roptrocerus \text{ sp. and } Cecidostiba \text{ spp.}$
$X_{2ij} = T. \text{undatulus}$	$X_{6ij} = Medetera \text{ spp.}$
$X_{3ij} = T. \text{chlorodia}$	$X_{7ij} = Belosta \text{ albipilosa}$
$X_{4ij} = C. \text{vancouverensis}$	

The coefficients (B 's) are estimated by linear regression. Regression coefficient/significant level (using the t -test are):

$B_0 = +4.472/.001$	$B_5 = -0.797/.081$
$B_1 = +0.062/.891$	$B_6 = -0.274/.074$
$B_2 = -3.690/.047$	$B_7 = -1.834/.001$
$B_3 = -0.670/.299$	$B_8 = +3.9016/.001$
$B_4 = -0.392/.001$	

The degree of fit of this function is indicated by multiple correlation coefficient $R^2 = 0.24$ and a standard deviation of 9.325. The regression function has accounted for 24 percent of the variation in the number of Douglas-fir beetles per sample. Most coefficients in the equation are of correct sign as indicated by their supposed effect, but the magnitude of the coefficients is smaller than expected. For example, *C. vancouverensis* is a parasite, so the coefficient B_4 should approach -1.0 (one less Douglas-fir beetle per sample for each *C. vancouverensis* per sample). The coefficient B_1 is of the wrong sign and is essentially zero. Both B_1 and B_3 are not significantly different from zero using Student's t -test and $\alpha = 0.10$ level for testing.

If coefficient B_8 for length of egg galleries was closer to 11.26, the coefficients of the other terms could be interpreted as the efficiency of that predator or parasite. The ratio of DFB progeny to length of egg galleries, under low pressure from entomophagous insects, is 11.26. Under this condition mortality would be $B_8 X_{8ij} - Y_{ij}$. At any value of B_8 , however, the coefficients still measure the relative effectiveness of one predator to another.

SAMPLING RECOMMENDATIONS

Measurements of Douglas-fir beetle attacks and survival provide useful population indices, which foretell tree mortality prior to fading of trees (Furniss and others 1979). When tempered with weather data and stand susceptibility, population measurements could alert forest managers of the need for intensive surveys and management actions up to a year ahead of present aerial detection surveys.

But where should samples be located? When should sampling occur and how many samples are needed? Some of these questions have been addressed before (Furniss 1962a, b; 1964). Samples taken closest to the time of emergence of beetle progeny will be correlated best with surviving population level (Furniss 1964). Fall sampling, however, is a practical compromise because mortality rate is fairly stable by then and work is more easily accomplished because roads are more accessible and weather is better than in early spring.

There is no single location in a tree that is representative of beetle attacks, progeny, and entomophagous insects. Due to the particular distributions of the Douglas-fir beetle and its two most abundant parasites and predators, future sampling should consist of a minimum of three locations per tree: (1) 4.6 m, (2) midpoint of the infested stem, and (3) about 3 m below the top of the infested stem to avoid the characteristic resinous, unsuccessful zone occurring near the top (Furniss 1962b). Using those sample locations, we calculate that it would require 4 and 30 trees to estimate average densities of progeny and egg galleries, respectively, per sample per tree, with $CV_{\bar{x}} = 0.20$.

If trees cannot be felled for sampling, an alternative might be to sample at 4.6 m height with a ladder and adjust average beetle density with a regression estimator, which in our study was $Y_i = 0.750 + 0.580 X_i$. In that case, we would have needed to sample 6 and 30 trees to estimate progeny and egg galleries, respectively, at the 4.6 m height with a $CV_{\bar{x}} = 0.20$. The sampler should note, however, that the regression estimator may differ in other infestations requiring additional sampling to calculate the regression coefficients.

The question of sampling individual species of entomophagous insects is more difficult. The problem is complicated by low densities of some; seasonal variations in their presence or absence; and their distributions. Accordingly, the sampler cannot assess them collectively at any one time or location. In order to measure their effects (density of surviving beetle progeny), however, sampling should occur after mortality has leveled off at the end of summer.

Nonetheless, if we take our samples from the three recommended heights, the numbers of trees required for a $CV_{\bar{x}} = 0.20$ for the seven categories of entomophagous insects are:

<i>Coeloides</i>	47 (37) ¹
<i>Medetera</i>	28 (27)
<i>Ecoclerus</i>	67 (64)
<i>Thanasimus</i>	595 (132)
<i>Temnochila</i>	37 (29)
<i>Roptrocerus, Cecidostiba</i>	85 (76)
<i>Belosta</i>	67 (56)

¹For comparison, numbers in parentheses are samples needed using data from 3-m intervals instead of three samples per tree.

CONCLUSIONS

The mathematical model based on the logistic function represents realistically the seasonal abundance of Douglas-fir beetle progeny in relation to regulatory factors involving entomophagous insects and sample characteristics. The model is useful for demonstrating the general importance of parasites and predators in the post-egg-hatch period. For example, average mortality of Douglas-fir beetle progeny after egg hatch in successfully attacked trees was 58 percent. Further improvement in the model should be directed toward separation of the proportional mortality due to entomophagous insects and that due to competition among progeny.

The information presented on the temporal and spatial distribution in trees of the Douglas-fir beetle and its major enemies will facilitate evaluation of infestations and development of an improved pest management program. Such a program will need to include information on susceptibility of surrounding trees and stands because that factor limits the amount of mortality that a particular population can cause. Research at this Station, in cooperation with Forest Service Region 1, and Idaho Department of Lands, is being directed to meet that need.

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Regression models were developed to predict abundance of Douglas-fir beetles in relation to entomophagous species, date, and sample characteristics. Probability of presence of entomophagous insects on samples was determined with the logistic function. Predation and parasitism were estimated to have caused 58 percent mortality of progeny during the summer.

KEYWORDS: Douglas-fir beetle, parasites, predators, sampling, modeling, logistic function.



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